

XVIII. *Further Observations on the Locomotor System of Medusæ.*

By GEORGE J. ROMANES, M.A., F.L.S., &c. Communicated by Prof. HUXLEY, Sec. R.S.

Received November 21, 1876,—Read January 11, 1877.

[PLATES 30 & 31.]

IN now submitting the second instalment of my observations on the locomotor system of Medusæ to the consideration of this Society, I should like to preface the communication with a few words to explain why several experiments which I had intended to perform this season have been unavoidably postponed. It is well known to naturalists that, from causes which are not very well understood, the numbers of Medusæ in the same localities are subject, in different years, to considerable variations. Now on the part of the coast where my work has throughout been carried on—viz. the Cromarty Firth, on the east of Scotland—the Medusæ have been this year as scarce as last year they were abundant. Probably the cause of this scarcity in the land-locked position occupied by the Cromarty Firth is in part to be attributed to the unusual prevalence of westerly winds which has this year been observable in that locality. But whatever the cause, the fact of this scarcity having existed has compelled me this year to restrict my observations, almost exclusively, to the genera *Sarsia*, *Tiaropsis*, and *Aurelia*. By way of introduction it is only necessary further to state that, for the sake of facilitating reference, I shall endeavour to construct the present communication on as nearly as possible the same general plan as the last one.

I. FUNDAMENTAL OBSERVATIONS.

§ 1. *Effects of excising the entire margins of Nectocalyces*.—Under this heading I have very little to add to the statements contained in my former paper. Many of the experiments which I have this year performed have necessitated, in a vast number of instances, the removal of the extreme periphery of nectocalyces; and in no one instance have I found an occurrence of even the slightest deviation from the general rule previously enunciated—the rule, namely, that “excision of the extreme margin of a nectocalyx causes immediate, total, and permanent paralysis of the entire organ”*.

§ 2. *Effects of excising the lithocysts from Gonocalyces (Umbrellas)*.—It will be remem-

* I may here mention, what perhaps I ought to have mentioned in my former paper, viz. that, in the case of the species *Tiaropsis diademata*, it frequently happens that a single quadrant of the thus mutilated nectocalyx bends slightly inwards at long intervals and without rhythm. I may also mention that I have this year performed the fundamental experiment on three additional species of the genus *Thaumantias*, viz. *T. purpureus* (Forbes), *T. crucifera* (Romanes), and *T. helicobostrica* (Romanes).

bered that excision of the eight marginal bodies of a covered-eyed Medusa is attended with the same degree of paralyzing effect as is the excision of the entire margin. It will also be remembered that this degree of paralyzing effect is not, generally speaking, so complete as it is in the case of the naked-eyed Medusæ; but that, after the operation, occasional contractions at long intervals are usually given, and that sometimes, though very rarely, these after contractions assume a rhythmical character more or less resembling the contractions of the unmutated animal. All the details concerning the behaviour of mutilated gonocalyces in this and in other respects were carefully recorded in my former communication. Afterwards, however, I had occasion to add a Postscript to that communication, in consequence of my attention having been drawn by Dr. LÜTKEN to a paper by Dr. EIMER, of the existence of which I was previously unaware. In this Postscript I had mainly to deal with certain discrepancies between Dr. EIMER's account of the behaviour of mutilated gonocalyces and that which I had given in my former communication. Now, as this want of complete accordance between Dr. EIMER's statements and those which I have published tends to cast doubt upon the accuracy of the latter, it becomes necessary for me in the present communication briefly to recur to the points wherein Dr. EIMER's results differ from my own. Of course it is needless to say that I have this year given my careful attention to these points, by repeating a great number of times the experiments which have reference to them. The following statements, therefore, may be considered final, so far as I am concerned.

The first point of difference to which I must allude is that which is explained in my Postscript thus:—"It will, of course, have been observed that Dr. EIMER's view as to the exact seat of spontaneity in *Aurelia aurita* does not coincide with mine. He is careful to state that the ganglionic function is distributed all round what he terms the 'contractile zone,' *i. e.* the crescent-shaped interruption of the margin in which the lithocyst, together with its gelatinous hood, is situated (see Plate 32). On the other hand, I have stated it as my opinion that the lithocyst is alone the locomotor centre; and notwithstanding the account which Dr. EIMER gives of the experiments by which he sought to localize that centre, I still adhere to this opinion. Dr. EIMER's experiments in this connexion were twofold:—First, that of progressively lessening the amount of contractile tissue left adhering to an excised segment of *Aurelia aurita*; and, second, that of excising the lithocyst without injuring the 'contractile zone.' Of these two methods Dr. EIMER appears to lay most stress upon the first one; for he merely mentions the second method in a short footnote towards the end of his paper, and there states that he only tried it in a few cases. Yet to me it seems that for the object in view the second method is much more trustworthy than the first. I am well aware of the fact pointed out by Dr. EIMER, that upon each contraction of a given segment of *Aurelia aurita* the two arms of the so-called 'contractile zone' approximate each other, and that this gives rise to the appearance of spontaneous action on their part. I think, however, that this appearance is deceptive, being caused only by the absence of resistance at the interrupted part of the margin to the pressure exerted by the contraction of

the immediately surrounding tissues. At any rate, so long as this possible explanation has not been thoroughly excluded by experiments conducted on the converse method of removing the lithocysts from between the arms of the contractile zone, so long, it seems to me, must the method we are considering be valueless. The question, then, must be decided by the converse method just alluded to, and by it alone. Now I have made experiments according to this method, and, so far as I remember, in every case, when sufficient care was taken to remove all the lithocysts, the contractile zone entirely ceased its contractions. And not only so, but by removing, with the aid of a well-pointed scissors, the little sac of crystals composing the central part of the lithocyst, without injuring the curious wing-like appendages by which this sac is partly surrounded*, and, conversely, by removing in other specimens these wing-like appendages alone, without injuring the little sac of crystals—by these experiments I was able to satisfy myself that the whole spontaneity of the lithocyst appeared to be exclusively lodged in (or about) the minute sac of crystals referred to.”

To these statements I have only to add that scores of experiments on *Aurelia aurita* have this year invariably confirmed those of last year. In no one instance have I been able to detect any physiological evidence of the presence of ganglionic matter in the “contractile zones.” In most instances, of course, occasional contractions were given after removal of the lithocysts alone; but I was never able to observe that the spontaneity in these instances proceeded more exclusively, or more frequently, from the contractile zones than from any other part of the general contractile tissue. For after allowing the animal to recover from the shock consequent upon removal of its lithocysts alone, and then observing the degree of spontaneity it manifested, I was in no case able to perceive that by now removing all the contractile zones, this degree of spontaneity was in the smallest degree diminished†.

This allusion to the spontaneity manifested by *Aurelia aurita* after its lithocysts have been removed, leads to the next point of difference between Dr. EIMER and myself. For the sake of conciseness, I shall again quote from my Postscript:—“I cannot quite assent to the description which Dr. EIMER gives of the contractions which sometimes supervene in the umbrella of *Aurelia aurita* when all the lithocysts have been removed. He describes them as ‘several *irregular, inefficient, and feeble* contractions of a local nature which rarely last any considerable time.’ This is no doubt partly true of some cases, but it is not true of all. I have frequently seen these after-contractions as rhythmical (though this is rare), as effectual, and as powerful as those which had been previously supplied by the single remaining lithocyst. Moreover, these contractions may usually be seen to emanate from some very localized portion of tissue, and from thence to radiate over the whole substance of the umbrella, just as the contractile waves which

* The “wing-like appendages” here referred to are shown by injection to be minute diverticula of the nutritive-tube system.

† [In this connexion I may observe that Mr. SCHÄFER has shown the “nerve-epithelium” to be exclusively confined to the region of the lithocysts.—1878.]

emanated from a single remaining lithocyst had previously done. On now cutting out this localized portion of tissue, the umbrella usually becomes again paralyzed, while the portion of tissue which previously animated it may be seen to continue its contractions after the manner of excised lithocysts. I did not pay sufficient attention to the number of hours after excision of the lithocysts during which these secondary movements continued, to admit of my speaking with confidence on this point; but, so far as I can recollect my numerous experiments with this species, it is certainly not correct to say that these contractions 'generally ceased after a few moments.' My impression is that they *usually* last for several days. I agree with Dr. EIMER, however, that, as a general rule, the secondary movements in *Aurelia aurita* are not so persistent as the primary ones; and also that in this species, under some circumstances*, insensibility to stimulation rapidly supervenes upon loss of spontaneity. This, however, is far from being the case with other species—for instance, *Cyanæa capillata* will continue to respond even to slight stimulation *two or three days* after it has been completely paralyzed by the removal of its lithocysts, and this even though it be kept in a small jar without change of water. Again, if the lithocysts be left *in situ* and the animal be kept in a confined body of water, irritability will continue for days after all the usual indications of spontaneity have disappeared. Nevertheless, with slight modifications, I have confirmed Dr. EIMER's experiment of placing different specimens of *Aurelia aurita* under similar conditions, removing the lithocysts of some and not of others, and observing that those individuals which had been operated upon died sooner than those which had not."

This year I have given careful attention to these secondary contractions manifested by the mutilated swimming-organs of *Aurelia aurita*; and as the fact of their occurrence will afterwards be found of importance in relation to some peculiar points in the physiology of this animal, I shall here detail all the observations regarding the subject which I have been able to make. In the first place, the above-quoted statements with reference to *Aurelia aurita* have been this year, with one exception, fully confirmed by numerous experiments. The one exception refers to my statement as to having "frequently seen these after-contractions as rhythmical (though this is rare), as effectual, and as powerful as those which had been previously supplied by the single remaining lithocyst." The word "rare" here, as applied to the rhythmical nature of these after-contractions, is not sufficiently strong. If I had said "very" or "exceedingly rare," the statement would have been more accurate. For although, so far as I can remember, the statement as it stands would apply without correction to *Cyanæa capillata*†, I have not this year found it to do so in the case of *Aurelia aurita*. The after-contractions of this species are nearly always, as Dr. EIMER describes them, "irregular;" that is to say, they nearly always occur at uncertain intervals. These intervals are

* That is, in particular, too high a temperature and want of aëration.

† I must trust to memory here, because I was not able this season to obtain a single specimen of this species.

usually very long, though different individuals manifest considerable difference in this respect, in some cases a great many more contractions occurring in a given time than in other cases. It is not unfrequently observable that these after-contractions occur in pairs, and more rarely in triplets; and when this is the case the interval of diastole corresponds with that which occurs in ordinary swimming.

So much for the rhythmical nature of these after-contractions of *Aurelia aurita*. With regard to their other qualities, I have nothing further to add. I am still unable to say that they appear to me either more "inefficient" or more "feeble" than the contractions which proceed from a single remaining lithocyst of average potency, particularly if the comparison be made between the former and the latter after a pause of a minute or more has in each case intervened between the contractions observed and the previous contraction (see III. (A) (a)). I have also been unable to perceive that the secondary contractions are any more of a "local" nature than are the primary ones. In almost every instance which I have this year observed, the description just quoted from my Postscript was strictly applicable; and those comparatively few instances in which the secondary contractions were local, were not much, if at all, more numerous than those in which primary contractions proceeding from a single remaining lithocyst were local. Again, my experience has this year been quite at variance with that of Dr. EIMER as regards the time after removal of the lithocysts during which the secondary movements persist. Numerous experiments have shown that it certainly is not correct to say that these contractions "generally cease after a few moments," or even "after several hours." Indeed so far have I found it from being true that they "rarely last any considerable time," that I am now able fully to confirm my original "impression," and to state positively that these after-contractions of *Aurelia aurita* "usually last for several days." For in some dozens of experiments I have found no exception to the rule that, if an ordinarily fair chance be given to the mutilated animals by keeping them in a basin-shaped vessel at a temperature not greatly above that of the sea and changing the water once a day, these secondary contractions persist for one day at the least, generally for two or three days, and sometimes longer. In most cases they continue after decomposition of some parts of the tissues has set in, and even after such decomposition has proceeded to the extent of giving the latter a certain ragged appearance, which is due to portions disintegrating into shreds. These remarks apply to many cases in which, not the contractile zones merely, but the entire margin had been removed.

Lastly, with regard to the greater vitality of un mutilated covered-eyed Medusæ with their lithocysts *in situ* than those which have had these bodies removed, I have found my previous statement substantially correct. There are wonderful individual variations, however, in this respect; for sometimes the irritability of the paralyzed specimens will remain after that of un mutilated specimens which are exposed to exactly the same conditions has been destroyed by decomposition. Comparisons, therefore, in this respect can only be fairly made between detached segments of the same individual; and in this case it may be taken as a rule that the segments in which the lithocyst is

allowed to remain preserve their irritability longer than the segments from which the lithocysts have been removed. The greatest amount of endurance that I have met with in these experiments was in the case of an individual cut into eight segments, in such a way as to leave one lithocyst in the middle of each arc. Four of the segments were then deprived of their lithocysts, and the paralyzed and unparalyzed segments were left in the same basin at a temperature of about 45° F. The water was changed once in every twenty-four hours, and all the eight segments were perfectly healthy at the end of the sixth day. Next night, however, the temperature rose, and in the morning of the seventh day all the segments were dead.

I have dwelt thus at length upon the differences between the results yielded by Dr. EIMER's experiments and those yielded by my own, because, although these differences refer to points that were of minor importance at the time when Dr. EIMER published his paper—a fact which, doubtless, led this observer, so well skilled in dealing with the great and peculiar difficulties that attend such an investigation of these and allied organisms, to neglect repeating these subordinate experiments a sufficient number of times,—still it will shortly be seen that, at the stage which the inquiry has now reached, it is of great importance to be in possession of accurate and precise data with regard to the points which we have just been considering*.

* [I here withdraw from the proof a footnote mentioning the fact that I had obtained histological evidence of the presence of nerve-cells and fibres in *Aurelia aurita*. I withdraw this note because it is now rendered superfluous by the much more extended and detailed histological researches of my friend Mr. SCHÄFER. Perhaps, however, it is desirable to state that my own histological work was merely of a cursory nature, sufficient only to show that there was here a splendid field for further cultivation. In accordance with my original plan, however, I deferred all systematic inquiry concerning the histological part of the subject till the more important of the physiological experiments should have been completed—not because I underrated the importance of a thorough re-investigation of the histology of the Medusæ, but, on the contrary, because I deemed such a re-investigation to be of so much importance that I hoped best to give it the attention which it deserved by postponing this difficult part of the inquiry until I should be able to devote to it my undivided attention. But as the physiology of the subject continued to open up more and more, I felt it was undesirable, either, on the one hand, to suspend this part of the inquiry, or, on the other hand, any longer to defer a careful development of the histological part. Accordingly I represented the case to Mr. SCHÄFER, who with great kindness consented to spend his leisure time in cooperating with me. The highly interesting character of the results which he has obtained show how desirable it was to render the histology of the Medusæ a subject of elaborate scrutiny; but as he has communicated these results to the Royal Society, it is unnecessary that I should here restate them. I may observe, however, that the elements which he describes were not unfamiliar to me, though I hesitated to pronounce with certainty upon their nervous character. But, lest the fibres which Mr. SCHÄFER describes as nervous should eventually prove to be the anatomical structures that are concerned in performing the physiological functions which I described in my former paper, I adopted in that paper a neutral term whereby to designate the nervous tracts whose presence my experiments, and also those of Dr. EIMER, had revealed. This neutral term was “lines of discharge,” a term which is applicable alike to partly or to fully differentiated nerves. And forasmuch as I still deem it premature to conclude that definite histological elements are concerned in the performance of these physiological functions, I think that while treating of the latter it still remains desirable to designate their structural correlatives by some such neutral term as “lines of discharge,” rather than by any term of a more precise signification.

I may also take this opportunity of observing that, almost simultaneously with the publication of Mr.

II. RHYTHM.

§ 1. *Relation between Size and Rhythm*.—It will be convenient here to introduce all the observations that I have been able to make with regard to the natural rhythm of the Medusæ. As Dr. EIMER has also made some observations in this connexion, before proceeding with the fresh points having relation to this subject, I shall consider those points to which allusion was made in my Postscript.

In *Aurelia aurita*, as Dr. EIMER has noticed, the rate of the rhythm has a tendency to bear an inverse proportion to the size of the individual. Size, however, is far from being the only factor in determining the differences between the rate of the rhythm of different specimens—the individual variations in this respect being very great even among specimens of the same size. What the other factors in question may be, however, I am unable to suggest.

§ 2. *Relations between the periods of Activity and the periods of Repose*.—Dr. EIMER affirms that the duration of the natural pauses, which in *Aurelia* sometimes alternate with bouts of swimming, bears a direct proportion to the number and strength of the contractions that occurred in the previous bout of swimming. In my Postscript I observed that *Sarsia* are much better adapted than *Aurelia* for determining whether any such precise relation obtains; for, in the first place, the strength of the contractions is more uniform, and, in the next place, the alternation of pauses with bouts of swimming is of a more decided character in *Sarsia* than in *healthy* specimens of *Aurelia*. I further observed that in *Sarsia* I was quite sure no such precise relation did obtain, although in a very general way it was true, as might be expected, that unusually prolonged bouts of swimming were sometimes followed by pauses of unusual duration. At that time I had not taken the trouble actually to count the pulsations and to time the intervals of rest, and so could not say any thing more upon the subject. This year, however, I have made precise observations with regard to this matter, and I find that they fully confirm my previous statements. As all the observations are very much the same, I shall only quote two of them:—

SCHÄFER's work, two other monographs have appeared on the histology of the nervous tissues of the Medusæ. One of these monographs is by Messrs. HERTWIG, and the other by Prof. EIMER. In my next paper I shall give an abstract of both, and shall therefore not burden this Postscript by endeavouring to do so at present. But I should like to take this the earliest opportunity of rectifying an injustice which, as I now learn from Prof. EIMER's last paper, I previously did him in my first paper. In my Postscript to that paper I stated that in our independent observations concerning the effect of excising lithocysts I had a right to claim priority, both as regards observation and publication. Prof. EIMER, however, now explains that, in consequence of his first paper having been bound in the Würtzburg Verhandlungen without its proper titlepage, the reference to the date of his work which occurs in the paper itself ("d. J.") refers, not to the year on the back of the volume, but to the year preceding. Therefore, although I was right in saying that I had anticipated Dr. EIMER in making the "fundamental observation," I was wrong in supposing that I had also anticipated him in publishing this observation. Dr. EIMER has thus a full right to claim priority as regards this and all his other researches concerning the nervous system of Medusæ.—1878.]

<i>Sarsia.</i>		<i>Sarsia</i> (another specimen).	
Number of pulsations.	Seconds of rest.	Number of pulsations.	Seconds of rest.
54	90	40	60
20	15	29	90
9	92	32	132
51	40	33	92
38	60	18	59
1	43	8	63
63	45	15	35
1	14	2	85
60	15	11	63
6	50	30	33
38	50	17	81
22	32	19	67
25	12	3	65
56	55	19	36
65	20	41	123
42	15	80	23
35	40	61	150
76	43	45	145
		40	120
		10	97
		14	35

These observations may be taken as samples of others which it would be unnecessary to quote, as it will be seen from the above that there is no precise relation between the number of the pulsations and the duration of the pauses. Nevertheless, that there is a *general* relation may be seen from some cases in which unusually prolonged pauses occur. The following instance will serve to show this:—

<i>Sarsia</i> (another specimen).	
Number of pulsations.	Seconds of rest.
38	30
22	35
49	40
30	45
46	20
2	15
24	380
112	20
45	185
894	30
6	45
4	140
2	185
30	240
200	60

In this case the relation between the long pause of 380 seconds and the subsequent prolonged swimming bout of 112 pulsations, is obvious. Also, as the latter was then followed by a short pause of 20 seconds and another comparatively short bout of 45 pulsations, the refreshing influence of the previous 380 seconds of rest may be supposed to have been not quite neutralized by the exhausting effect of the foregoing 112 pulsa-

tions. At any rate, looking to the general nature of the previous proportions (viz. in their sum $\frac{185}{211}$), it is certain that $\frac{380}{112}$ leaves a large preponderance in favour of nutrition, which preponderance is not much modified by adding the next succeeding proportion thus, $\frac{380+20}{112+45} = \frac{400}{157}$. Consequently, the organism may fairly be supposed to have entered upon the next prolonged period of rest (viz. 185 seconds) with a large balance of reserve power; so that when to this large balance there was added the further accumulation due to the further rest of 185 seconds, we are not surprised to find the next succeeding swimming-bout comprising the enormous number of 894 pulsations. But this great expenditure of energy seems to have been somewhat in excess of the energy previously accumulated by the prolonged rest; for this unusual expenditure seems next to have entailed an unusually prolonged period of exhaustion. At any rate it is plainly observable that the next succeeding proportions are greatly in favour of repose; for it is not until 360 seconds have elapsed, with only 12 pulsations in the interval, that energy enough has been accumulated to cause a moderate bout of 30 pulsations. But next another long and sustained pause of 240 seconds supervenes, and, the animal being now fully refreshed with a large surplus of accumulated energy, the next succeeding swimming-bout comprises 200 pulsations. Lastly there succeeded 60 seconds of rest, and here the observation terminated*.

§ 3. *Effects of Artificial Segmentation on the Rhythm.*—We have next to consider Dr. EIMER's observations concerning the effects on the rhythm of *Aurelia* which result on cutting the animal into segments; and here, again, I much regret to say that I cannot wholly agree with this author. It will be remembered that he says he found evidence of a very remarkable fact, viz. that by first counting the natural rhythm of an unmutated *Aurelia*, and then dividing the animal into two halves, one of these halves into two quarters, and one of these quarters into two eighths, the sum of the contractions performed by these four segments in a given time was equal to the number which had previously been performed in a similar time by the unmutated animal. And not only so, but the number of contractions which each segment contributed to this sum was a number that stood in direct proportion to the size of the segment; so that the half contracted half as many times, the quarter a quarter as many times, and the eighth parts one eighth part the number of times that the unmutated *Aurelia* had previously contracted in a period of equal duration. I am glad to observe that Dr. EIMER does not regard this rule otherwise than as liable to frequent exceptions; for, as already observed, I cannot say that my experiments have tended to confirm it. As stated in my

* If the reader takes the trouble to ascertain the average proportion between the number of pulsations and the seconds of rest in the first observations as far down as the first long pause, viz., as above stated, $\frac{185}{211}$, and if he then balances the succeeding income and expenditure of energy over all the rest of the observations, he will find the net result to accord very precisely with the proportion he previously obtained. But, as already stated, any such precision as this is certainly the exception rather than the rule.

It may here be stated that after the 60 seconds of rest above recorded, the animal began another swimming-bout. It was then immediately bisected, and the subsequent observations are detailed in the next footnote.

previous paper, there is a general tendency for the smaller segments of an *Aurelia* divided in this way to contract less frequently than the larger segments; and more careful observation this year has not resulted in establishing any more precise a relationship.

It would be tedious and unnecessary to quote my observations in this connexion; but as these observations brought out very clearly a fact which I had previously suspected, I may detail one experiment to illustrate this point. The fact in question is, that the *potency of the lithocysts* in any given segment of a divided *Aurelia* has more to do with the frequency of its pulsations than has the size of the segment. As mentioned in my other paper, one or more lithocysts may often be observed to be permanently prepotent over the others; and I may here observe that the segmentation experiments just described have shown the converse to be true, viz. that one or more lithocysts are often permanently feebler than the others. Well, if a specimen of *Aurelia* exhibiting decided prepotency in one or more of its lithocysts be watched for a considerable length of time, so as to be sure that the prepotency is not of a merely temporary character, and if the animal be then divided into segments in such a way that the prepotent lithocysts shall occupy the smaller segments, it may be observed, provided time be left for the tissues to recover shock, that the segments containing the prepotent lithocysts, notwithstanding their smaller size, contract more frequently than do the larger segments. Conversely, if the larger segments happen to contain feeble lithocysts, their contractions will be but few. I have, indeed, seen cases in which the lithocysts appeared to be quite functionless, so far as the origination of stimuli was concerned.

The following observations were made on a healthy specimen of *Aurelia* having all its lithocysts in good condition, but prepotency being well marked in the case of one of them, and also, though in a lesser degree, in the case of another. I divided the animal so as to leave one of these two prepotent lithocysts in each of the eighth-part segments, and the next most powerful lithocyst in the quadrant segment. In the following description I shall call the two eighth-part segments A and B, the former letter designating the segment containing the most powerful lithocyst. The *Aurelia* before being divided manifested for several hours a very regular and sustained rhythm of 32 per minute. After its division the various segments contracted at the following rates in one minute intervals:—

Time after operation.	Segment $\frac{1}{8}$.	Segment $\frac{1}{4}$.	Segment $\frac{1}{8}$ A.	Segment $\frac{1}{8}$ B.
$\frac{1}{2}$ hour.	20	25	27	15
1 „	20	25	27	15
2 hours.	29	25	27	16
4 „	19	16	27	12

Next morning the water which contained the segments was somewhat foul, and this, as is always the case, gave rise to abnormally long pauses. This effect was much more marked in the case of some of the segments than in that of others. I therefore observed the segments over five minutes intervals, instead of over one minute intervals as on the

previous day. The following is a sample of several such observations, all yielding the same general result.

Segment $\frac{1}{2}$.		Segment $\frac{1}{4}$.	Segment $\frac{1}{8}$ A.	Segment $\frac{1}{8}$ B.
Number of pulsations.	Seconds of rest.	No motion during the hour of observation.	Continued persistently to contract with a nearly perfect rhythm of 78 in the 5 minutes during the hour of observation.	Rhythm tolerably perfect at 78 in the 5 minutes; but this was occasionally interrupted by long pauses of 4 or 5 minutes duration.
12	120			
3	10			
2	20			
44	130			
12	20			
73	5 minutes.			
Average rate $14\frac{4}{5}$ per minute.		No motion.	Continuous rhythm at the rate of $15\frac{3}{5}$ per minute.	Interrupted rhythm at the rate of $15\frac{3}{5}$ per minute.

I now transferred all the segments to fresh sea-water, with the following results:—

Rhythm during first quarter of an hour immediately after transference, in five minutes' intervals.

Time.	Segment $\frac{1}{2}$.	Segment $\frac{1}{4}$.	Segment $\frac{1}{8}$ A.	Segment $\frac{1}{8}$ B.
First 5 minutes	139 (irregular).	0	83 (regular).	20 (irregular).
Second 5 minutes ..	0	0	68 "	75 (regular).
Third 5 minutes	100 (regular).	39 (irregular).	70 "	69 "

Rhythm 2 hours after transference (5 minutes' intervals).

Segment $\frac{1}{2}$.	Segment $\frac{1}{4}$.	Segment $\frac{1}{8}$ A.	Segment $\frac{1}{8}$ B.
82 (regular).	77 (regular).	70 (regular).	62 (regular).

Rhythm next day (5 minutes' intervals).

Segment $\frac{1}{2}$.	Segment $\frac{1}{4}$.	Segment $\frac{1}{8}$ A.	Segment $\frac{1}{8}$ B.
68	55	17	Dead.

Next day all the segments were dead except the largest one, in which a single lithocyst still continued to discharge at the rate of 24 in five minutes.

Now, with regard to these Tables it is to be observed that during the first day the prepotent lithocyst in the eighth-part Segment A maintained an undoubted supremacy over all the others, and that the same is true of the comparatively potent lithocysts in the quadrant. (This is not the case with Segment B; probably the degree of prepotency of the lithocyst in this case was not sufficient to counteract the antagonistic

influence of the small size of the segment.) But next day the supremacy of the small Segment A was not so marked; for although its rhythm was more *regular* in the stale water than was that of the largest segment, its actual number of contractions in a given time was just about equal to that of the largest segment. Again, after transference to fresh sea-water, the balance began to fall on the side of the larger segments; for even the quadrant, which in the stale water had ceased its motions altogether, now held a middle position between that of the half-segment and the prepotent eighth-part segment. On the next day, again, the balance fell decidedly in favour of the larger segments, and the weaker eighth-part segment died. Lastly, next day all the smaller segments were dead.

Hence the principal facts to be gathered from these observations are, that as time goes on the rhythm of all the segments progressively decreases, and that the decrease is more marked in the case of the smaller than in that of the larger segments. This lesser endurance of the smaller segments also finds its expression in their earlier death. Now as these smaller segments started with a greater proportional amount of ganglionic power than the larger segments, their lesser amount of endurance can only, I think, be explained by supposing that the process of starvation proceeds at a rate inversely proportional to the size of the segment—a supposition which is rendered probable if we reflect that the smaller the segment the greater is the proportional area of severed nutrient-tubes*. And in this connexion it is interesting to observe that, although the endurance of the smaller segments was less than that of the larger as regards the deprivation of nutriment, it was greater than that of the larger segments as regards the deprivation of oxygen. This is shown by the greater regularity of the rhythm mani-

* It may be thought that the greater area of general tissue-mass in the larger segments than in the smaller, and not the lesser proportional area of tube-section, is the cause of the larger segments living longer than the smaller ones. I am led, however, to reject this hypothesis, because in *Sarsia*, where segmentation entails a comparatively small amount of tube-section, there is no constant rule as to the larger segments showing more endurance than the smaller ones—the converse case, in fact, being of nearly as frequent occurrence. I can only account for this fact by supposing that the endurance of the segments of *Sarsia* is determined by the degree in which the three or four minute open tube-ends become accidentally blocked. This supposition is the only one I can think of to account for the astonishing contrasts as to endurance that are presented by different segments of the same individual, and, I may add, of different individuals when deprived of their margins and afterwards submitted to the same conditions. For instance, a number of equally vigorous specimens had their margins removed, and were then suspended in a glass cage attached to a buoy in the sea. Four days afterwards some of the specimens were putrid, while others were as fresh as they were when first operated on. Again, as an instance of the experiments in segmentation of *Sarsia*, I may quote an experiment in which a score of specimens were divided in all sorts of ways, such as leaving the polypite attached to one half, or three marginal bodies in one portion and the remaining marginal body in the other portion, &c., &c. Yet, although it was very exceptional to find the two portions presenting an equal degree of endurance, no uniform results pointing to the cause of the variations could be obtained. In most cases, however, the energy, as distinguished from the endurance, of the larger segments was conspicuously greater than that of the smaller. But it is curious that in many cases the effects of *shock* appeared to be more marked in the larger than in the smaller segments—the latter, for some time after the operation, contracting much more frequently than the former. To show both these effects, one

fed by the smaller than by the larger segments in the stale water; and the fact is presumably to be accounted for by the consideration that the ganglia in the smaller segments were more potent than those in the larger.

experiment may be quoted. A specimen of *Sarsia* was divided into two parts, of which one was a quadrant. Immediately after the operation the results were as follows:—

Portion $\frac{1}{4}$.		Portion $\frac{3}{4}$.	
Number of pulsations.	Minutes of rest.	Number of pulsations.	Minutes of rest.
20	0	0	5
4	4	10	2
15	5	46	1
6	3	23	2
		49	1
45	12	900	1
		117	1
		1145	13

To show the difference between the *endurance* of two halves of a bisected specimen of *Sarsia*, I may quote one experiment which was performed on the same specimen as the one mentioned in the text to show the general relationship between the duration of the pauses and that of swimming-bouts (see last footnote).

Immediately after Bisection.

$\frac{1}{2}$ A.		$\frac{1}{2}$ B.	
Number of pulsations.	Seconds of rest.	Number of pulsations.	Seconds of rest.
56	10	82	180
150	150	51	20
68	335	14	60
130	30	13	50
46	45	46	45
2	10	38	65
99	66	18	45
103	360	23	60
12	4	35	130
		105	70
Pauses now become longer, and swimming-bouts shorter.			

Twenty-four hours after the Operation.

$\frac{1}{2}$ A.		$\frac{1}{2}$ B.	
Number of pulsations.	Seconds of rest.	Number of pulsations.	Seconds of rest.
2	363	50	20
12	362	81	25
4	666	37	101
25	300	2400	60

With regard, therefore, to the original point under consideration, I conclude that although the size of the segments is doubtless one factor in determining the relative frequency of contraction, there are at least two other factors quite as important, viz. the relative potency of the lithocysts, and the length of time that elapses between performing

But although in the case of *Sarsia* the lesser endurance of the smaller segment than of the larger cannot be regarded as a general rule, it may be so regarded, as already stated, in the case of *Aurelia*. The following experiment exemplifies this particular rule even more prettily than does the one quoted in the text, from the fact that the segments survived the operation for a greater number of days.

An *Aurelia* having a regular and well-sustained rhythm of 20 per minute was divided as already described in the text. In five minutes' intervals on successive days the average rates of the four segments were as follows:—

Four hours after the Operation.			
Seg. $\frac{1}{2}$.	Seg. $\frac{1}{4}$.	Seg. $\frac{1}{8}$ A.	Seg. $\frac{1}{8}$ B.
100	100	85	90
Next Day.			
88	90	64	58
Next Day.			
86	82	62	57
Next Day.			
59	45	24	20
Next Day.			
50	49	20	10
Next Day.			
43	33	18	4
Next Day.			
39	32	19	Dead.
Next Day.			
33	7	Dead.	0
Next Day.			
28	Dead.	0	0

Next day the temperature unfortunately rose sufficiently to cause the death of the single surviving segment, which otherwise would probably have lived for one or two days longer.

the operation and observing the rhythm. Hence it is that in my experience I have found but very few examples of Dr. EIMER's rule.

§ 4. *Effects of other forms of Mutilation on the Rhythm.*—The next point I have to dwell upon is one of some interest. If the polypite of *Aurelia*, or of any other covered-eyed Medusa, be suddenly cut off at its base, the swimming-motions of the umbrella immediately become accelerated*. This acceleration, however, only lasts for a few minutes, when it gradually begins to decline, the rate of the rhythm becoming slower and slower, until, finally, it comes to rest at a rate considerably less than was previously manifested by the unmutilated animal. If a circular piece be now cut out from the centre of the umbrella, the rhythm of the latter again becomes temporarily quickened, but, as before, gradual slowing next supervenes. This slowing, however, proceeds further than in the last case; so that the rate at which the rhythm next becomes stationary is even less than before. If, now, another circular ring be cut from the central part of the umbrella,—*i. e.* if the previously open ring into which this organ had been reduced by the former operation be somewhat narrowed from within,—the same effects on the rhythm are again observable; and so on with every repetition of the operation, the rate of the rhythm always being quickened in the first instance, but then gradually slowing down to a point somewhat below the rate it manifested before the previous operation. It will here suffice to quote one experiment among many I have made in this connexion:—

An <i>Aurelia</i> manifested a regular and sustained rhythm of	26
Immediately after removal of polypite, rhythm rose to	36
Rate then gradually fell for $\frac{1}{4}$ of an hour, and became stationary at	20
Circular incision just including ovaries caused rhythm to rise to	26
After gradual fall during $\frac{1}{4}$ of an hour, rhythm became stationary at	17
Another circular incision carried round midway between the former one and the margin caused rhythm to rise to	24
Rate again gradually declined, and in $\frac{1}{4}$ of an hour was	12
Another circular incision was carried round as close to the margin as was compatible with leaving the physiological continuity of all the litho- cysts intact. Rhythm rose to	14
Within a few minutes it fell to	6

Excepting the cases where the effects of shock are apparent, some such series of phenomena as those just recorded are always sure to ensue when a covered-eyed Medusa is mutilated in the way described†. But this kind of mutilation, besides producing such marked effects on the *rate* of the rhythm, also produces an effect in impairing the *regularity* of the rhythm. In some specimens the latter effect is more marked than it

* In some cases this effect is obliterated by that of shock, the swimming-motions ceasing altogether for a time, or becoming more feeble.

† I have not tried any experiments with the naked-eyed Medusæ in this connexion.

is in others. The following series of observations will serve to render a good idea of this effect:—

An *Aurelia* manifested a regular and sustained rhythm of 36. Immediately after the removal of the polypite the rate of rhythm in successive minutes was as follows:—40, 39, 37, 35, 32, 30, 29, 26, 24, 18, 14 (40 seconds' pause), 16, 15, 14, 15, 16 (40 seconds' pause), 22, 20, 19, 15, 16, 17, 14, 13, 13, 15, 16, 16, 17, 18, 14, 12, 13, 11, 12, 9, 15, 16, 14, 12, 9, &c., the rhythm now continuing very irregular. An hour after the operation the following were the number of contractions given in one-minute intervals, the observations being taken at intervals of ten minutes:—15, 15, 12, 22, 14, &c.

In this experiment, therefore, as soon as the acceleration-stage had been passed, viz. about a quarter of an hour after the operation, a great disturbance was observable in regularity of the rhythm; for before the removal of the polypite the Medusa had been swimming for hours with perfect regularity.

It is an important point in connexion with these observations to ascertain whether the remarkable effects of mutilation on the rhythm are transitory or permanent; but as yet I have not been able to determine this point with certainty. So far as my observations have gone, they all tend to prove that the slowing-effect of the mutilation is permanent; but I do not like as yet to say positively that it is so, because even un mutilated specimens of *Aurelia* sometimes slow their rhythm from day to day when kept in confinement. I may here state, for the benefit of those who may repeat these experiments, that when an *Aurelia* is converted into an open ring, the various parts of the ring fall together, especially if it be a narrow one. This unnatural state of things, in consequence of the irritation arising from the different parts of the ring rubbing on one another, causes the remnant of the animal to quicken its swimming-motions. Nor is this source of fallacy obviated by keeping the open ring distended by means of some cylindrical body of appropriate diameter; for the presence of this foreign body acts more or less as a constant stimulus. The best plan, therefore, to adopt is to make the circular incisions only through the thickness of the very tenuous nervo-muscular sheet, leaving the gelatinous tissue everywhere intact. The natural shape of the animal is thus not in the least affected, while the constituent parts of the nervo-muscular sheet are physiologically separated from one another as effectually as if the one were altogether removed from the other.

Before concluding my description of these experiments, it may perhaps be as well to mention one other, which was designed to meet a possible objection to the inferences which, as I shall presently explain, these experiments seem to sustain. It occurred to me, as a remote possibility, that the slowing and irregularity of the rhythm, which are observable about a quarter of an hour after the operations described, might be due to the deprivation of adequate nourishment suffered by the ganglia, in consequence of the escape of nutrient matter from the cut ends of the nutrient tubes. Accordingly, instead of cutting off the polypite, I tried the effect of momentarily immersing it in hot

water, and found, as I had expected, that the subsequent disturbances of the rhythm were precisely similar to those which result from removal of the polypite.

Now, to draw any inferences from such meagre facts as the above would be hazardous, unless we recognize that in so doing our inferences are not trustworthy. But, with this recognition, I think there will be no harm in briefly stating the deductions to which the facts, such as they are, would seem to point.

Physiologists are undecided as to the extent in which many apparently automatic actions may not really be actions of a reflex nature. Given, for instance, any ganglio-muscular tissue which is rhythmically contracting, and how are we to know whether the action of the ganglia is truly automatic, or sustained from time to time by stimuli proceeding from other parts of the organism? In most cases experiments cannot be conducted with reference to this question, but in the case of the Medusæ they may be so; and it was with the view of throwing light on this question that the experiments just described were made. Now in these experiments the fact is sufficiently obvious that mutilations of any part of the organism modify the rhythm of the marginal ganglia most profoundly. That this modification does not proceed from shock, would seem to be indicated by the facts that the first effect of the mutilation is to *quicken* the rhythm, that there is a sort of general proportion to be observed between the amount of tissue abstracted and the degree of slowing of the rhythm produced, and that the slowing effects continue for so long a time. All these facts seem to show that we have here something other than mere shock to deal with. A strong suspicion, therefore, arises that the cause of the slowing of the rhythm which results from removing the polypite, or a part of the general contractile tissue of the bell, consists in the destruction of some influence of an afferent character which had previously emanated from the parts of the organism which have been removed; and that the normal rhythm before the operation was partly due to a continuous reception, on the part of the ganglia, of this afferent or stimulating influence. In support of this view are the facts that the first effect of such an operation as we are considering is greatly to accelerate the rhythm, and that this acceleration then gradually declines through a period of about a quarter of an hour. These facts tend to support this view, because, if it is correct, they are what we might anticipate. If the polypite, for instance, while *in situ*, is continually supplying a gentle stimulus to the marginal ganglia, when it is suddenly cut off, the nerve-tracts through which this stimulating influence had previously been conveyed must be cut through; and as it is well known how irritable nerve-fibres are at their points of section, it is to be expected that the irritation caused by cutting these nerve-tracts, and probably also the action of the sea-water on their cut extremities, would cause them to stimulate the ganglia more powerfully than they did before their mutilation. And here I may state that on several occasions, with vigorous specimens, I have observed a sudden removal of the polypite to be followed, not merely with a quickening of the rhythm on the part of the bell, but with a violent and long-sustained spasm. Again, as regards the other fact before us, it is obvious that as soon as the cut extremities of the nerves begin to die down, and so

gradually to lose their irritability, the effect on the rhythm would be just what we observe it to be, viz. a gradual slowing till the rate falls considerably below that which was exhibited by the unmutilated animal. And even the *irregularity* which is at this stage so frequently observable is, I think, what we should expect to find if this view as to the essentially reflex character of the natural rhythm is the true one.

If this view is the true one, the question next arises as to the nature of the process which goes on in the excitable tissues, and which afterwards acts as a stimulus on the ganglionic tissues. This question, however, I am quite unable to answer. Whether the process is one of nutrition, of oxygenation, of chemical changes exerted by the seawater, or a process of any other kind, further experiments may perhaps be able to show; but meanwhile I have no suggestion to offer.

§ 5. *Effects of lessening the amount of Tissue adhering to a single Ganglion**.—The above experiments led me to try the effects of cutting out a single lithocyst of *Aurelia*, and, after the rhythm of the detached segment had become regular, progressively paring down the contractile tissues around the ganglion. I found that this process had no very marked effect on the rhythm until the paring reached within an inch or two of the ganglion. Then, however, the effect began to show itself, and with every successive paring it became more marked. This effect consisted in slowing the rate of the rhythm, but more especially in giving rise to prolonged pauses. Indeed, if only a very little contractile tissue was left adhering to the ganglion, the pauses often became immensely prolonged; so that one might almost suppose the ganglion to have entirely ceased discharging. But if a stimulus of any kind were then applied, the rhythmic discharges at once recommenced. They then generally continued for some little time at a slower rate than that which they had manifested before they were affected by the paring down of the contractile tissue. To illustrate these effects, it will suffice to quote one experiment from my notes:—“In an eighth-part segment of *Aurelia*, measuring 5 inches by 4, the rhythm for several hours was quite regular at 18 per minute. A band of tissue measuring half an inch across was now removed from each side of the segment. Rate immediately rose to 22, and then gradually fell again to 18. Another similar band was now removed. This operation was followed by a pause of several minutes' duration, after which some irregular contractions occurred; but eventually these gave place to a regular rhythm of 16 per minute. The tissue-cone was now truncated by cutting off an inch of its apex. The rate of rhythm rose to 18, and eventually became regular at 13. On now again truncating the cone, by removing from its upper part a band of tissue half an inch wide, the rate again rose slightly, but then became stationary at 10. Lastly, a band of tissue half an inch wide was removed from both the sides of the truncated cone, thus reducing the contractile tissue surrounding the lithocyst to a small piece measuring $\frac{5}{8}$ of an inch long by $\frac{1}{2}$ an inch broad. This final operation was followed by prolonged periods of

* In view of more recent observations on the histology of lithocysts, I substitute in this paper the term “ganglion” for the term “locomotor centre,” which in my previous paper I everywhere used to denote these bodies.

quiescence, which were broken by occasional single contractions and occasional bouts of partly rhythmical swimming-motions. These bouts could at any time be pretty certainly evoked by a stimulus, and the rate of their imperfect rhythm was about 10 per minute."

§ 6. *Effects of Temperature on Rhythm.* (a).—The effects of temperature on the rhythm of Medusæ are very decided. For instance, a specimen of *Sarsia* which in successive minutes gave the following numbers of pulsations—16, 26, 0, 0, 26, gave 60 pulsations during the next minute, while a spirit-lamp was held under the water in which the Medusa was swimming. If hot water be added to that in which *Sarsia* are contained until the whole is about milk-warm, their swimming-motions become frantic. If the same experiment be performed after the margins of the *Sarsia* have been removed, the paralyzed bells remain quite passive, while the severed margins exhibit the frantic motions just alluded to.

In the case of *Aurelia aurita* the characteristic effects of temperature on rhythm may be better studied than in that of *Sarsia*, from the fact that the natural motions are more rhythmical and sustained in the former than in the latter genus. I have therefore, in this connexion, made more observations on *Aurelia* than on *Sarsia*. The following, quoted from my notes, may be taken at a typical experiment:—

"A small and active specimen of *Aurelia* contracted with the greatest regularity 33 times per minute in water kept at 34°; but on transference to water kept at 49°, the contractions always became irregular, in respect (a) of not having a perfectly constant rhythm, and (b) of exhibiting frequent pauses, which was never the case in colder water. The rate of rhythm in the warmer water varied from 37 to 49; and, as in these observations no allowance was made for the occurrence of the pauses, the actual rate of rhythm during the swimming-motions was about 60 per minute. The following are some sample observations in the case of this specimen:—

Rate of Rhythm in successive Minutes.

Temperature of water (Fahr.).	Number of pulsations.	Seconds of rest.
49°	41	5
"	49	4
Transferred to 34	33	0
"	33	0
"	33	0
"	33	0
Transferred to 49	45	4
"	39	10
"	37	15
Transferred to 34	20	0
"	30	0
"	33	0
"	33	0
"	33	0
"	33	0

"This rate continued quite regularly for a quarter of an hour, when the observation terminated."

It might naturally be supposed that when the alterations of temperature between 34° and 49° produce such marked effects on the rhythm, still greater alterations would be attended with still greater effects. Such, however, is not the case. Water at 70° or 80°, for instance, has the effect of permanently *diminishing* the rate of the rhythm, after having temporarily raised it for a few seconds. The following note will serve to convey a just estimation of these facts:—

"An *Aurelia*, whose rhythm in water at 40° was very regular at 18 per minute, was suddenly transferred to water at 80°. In the immediately succeeding minutes the rhythm was 22, 20, 14. The latter rate continued for nearly half an hour, when the observation terminated."

The effect of very warm water, therefore, is to slow the rhythm, as well, I may add, as to enfeeble the vigour of the contractions. The case of Medusæ thus differs, in the former respect, from that of the heart; and I think the reason of the difference is to be found in the following considerations. Even slight elevations of temperature are quickly fatal to the Medusæ, so it becomes presumable that considerable elevations act very destructively on the nervo-muscular tissues of these animals. This destructive effect of high temperatures may therefore very probably counteract the stimulating effect which such temperatures would otherwise exert on the natural rhythm; and hence a point would somewhere be reached at which the destructive effect would so far overcome the stimulating effect as to slow the rhythm instead of quicken it. That this is probably the true, as it certainly is the only explanation to be rendered, will, I think, be conceded when I further state that if an *Aurelia* be left for some little time in water at 80° and then again transferred to water at 30° or 40°, its original rate of rhythm at the latter temperature does not again return, but the rhythm remains permanently slowed. And, in favour of the explanation just offered, it may be further pointed out that the first effects of sudden immersion in heated water is to *quicken* the rhythm—it not being for a few seconds, or for even a minute or two after the immersion, that the rhythm becomes slowed. Lastly, the slowing takes place gradually; and this is what we should expect if, as is probable, the destructive effect takes somewhat more time to become fully developed than does the stimulating effect.

(b) *Cold*.—Before leaving the subject of temperature in relation to rhythm, I must say a few words on the effects of cold. The following may be regarded as typical experiments:—

"An *Aurelia* presenting a regular rhythm of 20 per minute in water at 45° was placed in water at 19°. Soon after the transference the rhythm began to slow, and the strength of the contractions to diminish. Both these phenomena rapidly became more and more pronounced, till the rhythm fell to 10 per minute (still quite regular), and the contractions ceased to penetrate the muscular tissue further than an inch or so from the marginal ganglia. Shortly after this stage pauses became frequent; but

mechanical or other irritation always originated a fresh swimming-bout. Next only one very feeble contraction was given at long and irregular intervals—a contraction so feeble that it was restricted to the immediate vicinity of the lithocyst in which it originated. Soon after this stage irritability towards all kinds of stimuli entirely ceased, including even strong spirit dropped on the under surface of the animal when taken momentarily out of the water. All these stages thus described were passed through rapidly, the whole series occupying rather less than five minutes. On now leaving the specimen for ten minutes and then restoring it to its original water at 45°, all the above-mentioned stages were passed through in reverse order. The first faint marginal contraction occurred four minutes after restoration to the warmer water. This contraction was confined to the immediate vicinity of the prepotent lithocyst, and all subsequent contractions continued to be so for the next three minutes. Rhythm very slow. Contractions now began to penetrate round the margin, and in eight minutes from the restoration had gone all the way round, the rate of their rhythm meanwhile increasing. In two minutes more all the umbrella was contracting at the rate of 15 per minute."

In another specimen, subjected to the same conditions, the rate of recovery was even more rapid, occupying only two minutes altogether; but in every case the process of recovery is a gradual one, and differs only in the time it occupies in passing through the various stages.

(c) *Effects of freezing Medusæ.*—In conclusion I will describe some rather interesting experiments that consisted in freezing some specimens of *Aurelia* into a solid block of ice. Of course, as sea-water had to be employed, the cold required was very considerable; but I succeeded in turning out the Medusæ encased on all sides in a continuous block of frozen sea-water. By now immersing this block in warm water, I was able to release the contained specimens, which then presented a very extraordinary appearance. The thick and massive gelatinous bell of a Medusa is, as every one knows, chiefly composed of sea-water, which everywhere enters very intimately into the structure of the tissue. Now all this sea-water was, of course, frozen *in situ*; so that the animals were everywhere and in all directions pierced through by an innumerable multitude of ice crystals, which formed a very beautiful meshwork pervading the whole substance of their transparent tissues.

These experiments were made in order to ascertain whether the Medusæ, after having been thus completely frozen, would survive on being again thawed out; and, if so, whether the freezing process would exert any permanent influence on the rate of their rhythm. Now in all the cases the Medusæ after having been thawed out presented a ragged appearance, which was due to the disintegrating effect exerted by the ice crystals while forming in the tissues; yet, notwithstanding this mechanical injury superimposed on the physiological effects of such extreme cold, all the Medusæ recovered on being restored to sea-water of the normal temperature. The time occupied by the process of recovery varied in different individuals from a few minutes to half an hour or more; and it was observable

that those specimens which recovered soonest had the rate of their rhythm least affected by the freezing. In no case, however, that I observed did the rate of the rhythm after the freezing return fully to that which had been manifested before the freezing.

§ 7. *Effects of certain gases on the Rhythm.* (a) *Oxygen*.—I will now conclude my remarks on rhythm by very briefly describing the effects of certain gases. Oxygen forced under pressure into sea-water containing *Sarsia* has the effect of greatly accelerating the rate of their rhythm. The following observation on a single specimen will serve to render this apparent.

Number of pulsations given by *Sarsia* in successive five minutes' intervals.

In ordinary sea-water	472, 527, 470
In oxygenated sea-water	800
In ordinary sea-water	268, 350, 430

It will be seen from this observation that the acceleration of the rhythm due to the oxygenation was most marked. Indeed the pulsations followed one another so rapidly that it was no easy matter to count them. It must also be stated that while the animal was under the influence of oxygen, the duration of the natural pauses between the swimming-bouts was greatly curtailed—the swimming-motions, in fact, being almost quite continuous throughout the five minutes that the Medusa was exposed to such influence. Lastly, it will be observed from the above Table that the unnatural amount of activity displayed by the organism while in the oxygenated water entailed on it a considerable degree of exhaustion, as shown by the fact that even a quarter of an hour after its restoration to normal water its original degree of energy had not quite returned.

(b) *Carbonic acid*.—As might be expected this gas has the opposite effects to those of oxygen. It is therefore needless to say more about this agent, except that if administered in large doses it destroys both spontaneity and irritability. Nevertheless, if its action is not allowed to last too long, the Medusæ will fully recover on being again restored to normal sea-water.

(c) *Nitrous oxide*.—This gas at first accelerates the motions of *Sarsia*, but eventually retards them. I omitted, however, to push the experiment to the stage of complete anæsthesia, which would doubtless have supervened had the pressure of the gas been sufficiently great.

(d) *Deficient aëration*.—It may now be stated that the Medusæ are exceedingly sensitive to such slight carbonization of the water in which they are contained as results from their being confined in a limited body of it for a few hours. The rhythm becomes slowed and the contractions feeble, while the pauses between the swimming-bouts become more frequent and prolonged. If the water is not changed, all these symptoms become more marked, and in addition the rhythm becomes very irregular. Eventually the swimming-motions entirely cease; but almost immediately after the animals are restored

to normal sea-water, they recover themselves completely, the rate and regularity of their rhythm being then quite natural. The suddenness with which this return to the normal state of things is effected cannot but strike the observer as very remarkable; and, I may observe, it takes place with equal suddenness at whatever stage in the above-described process of asphyxiation the transference to normal sea-water is accomplished*.

III. STIMULATION.

Under this heading I have a great number of fresh results to communicate; and as these chiefly have reference to electrical stimulation, I think it will be convenient to modify the order observed in my last paper, and to consider the other modes of stimulation first.

§ 1. *Mechanical stimulation*.—The only remark I have to make in this connexion is, that when the paralyzed swimming-organ of *Aurelia aurita* is stimulated by a single mechanical irritation, it often responds with two, and more rarely with three contractions, which are separated from one another by an interval of about the same length as the normal diastole of the unmutilated animal.

§ 2. *Chemical stimulation*.—Dilute spirit, or other irritant, when dropped on the paralyzed swimming-organ of *Aurelia aurita*, often gives rise to a whole series of rhythmical pulsations, the systoles and diastoles following one another at about the same rate as is observable in the normal swimming-motions of the unmutilated animal.

§ 3. *Thermal stimulation*.—It is somewhat difficult, in the case of paralyzed swimming-organs, to prove the occurrence of a contraction in response to thermal stimulation, from the fact that while these tissues are not nearly so sensitive to this mode of excitation as might be anticipated, they are, as observed in my former paper, extraordinarily sensitive to mechanical excitation. It therefore becomes difficult to administer the appropriate thermal stimulus without at the same time causing a sufficient mechanical disturbance to render it doubtful to which of the stimuli the response is due. This may be done, however, by allowing a few drops of heated sea-water to run over the excitable surface while it is exposed to the air. In this and in other ways I have satisfied myself that the paralyzed tissues of swimming-organs respond to sudden elevations of temperature.

§ 4. *Luminous stimulation*.—It is interesting to note that, in the case of some of the naked-eyed Medusæ, the action of light as a stimulus is most marked and unfailing. In the case of *Sarsia*, for instance, a flash of light let fall upon a living specimen almost invariably causes it to respond with one or more contractions. If the animal is vigorous and swimming freely in water, the effect of a momentary flash thrown upon it during one of the natural pauses is immediately to originate a bout of swimming. But if the animal is non-vigorous, or if it is removed from the water and spread flat upon an object-glass, it usually gives only one contraction in response to

* Dr. EIMER has also observed the facts mentioned in this paragraph (*d*).

every flash. There can thus be no doubt that a sudden transition from darkness to light acts upon *Sarsia* as a stimulus, and this even though the transition be but of momentary duration. The question therefore arises as to whether the stimulus consists in the presence of light, or in the occurrence of the sudden transition from darkness to light and from light to darkness. To answer this question I tried the converse experiment of placing a vigorous specimen in sunlight, waiting till the middle of one of the quiescent stages in the swimming-motions had come on, and then suddenly darkening. In no case, however, under these circumstances, did I obtain any response; so that I cannot doubt it is the light *per se*, and not the sudden nature of the transition from darkness to light, which in the former experiment acted as the stimulus. Indeed the effect of the converse experiment just described is rather that of inhibiting contractions; for, if the sunlight be suddenly shut off during the occurrence of a swimming-bout, it frequently happens that the quiescent stage immediately sets in. Again, in a general way, it is observable that *Sarsia* are more active in the light than they are in the dark, the comparative duration of the quiescent stages being less in the former than in the latter case. Light thus appears to act towards these animals as a constant stimulus. Nevertheless, when the flashing method of experimentation is employed, it is observable that the stimulating effect of the flashes progressively declines with their repetition—supposing, of course, that the intensity of the light employed remains constant, and that the rate at which the flashes are thrown in is not so slow as to cause the ganglia to forget, as it were, the occurrence of the previous flash before its successor is thrown in. It is difficult to measure with any exactness the limit of time during which the effect of the previous flash remains, but it appears to be about a quarter of a minute; for if the flashes are thrown in with a greater frequency than this, the progressive decline in their efficiency as stimulants first becomes observable. In all cases the response of *Sarsia* to luminous stimulation appears to be quite as rapid as is their response to any other mode of stimulation, although, as I have not in the case of this genus been able to measure the period of latent stimulation, this statement rests only on the estimate formed by the eye. It is further to be observed that when the efficacy of luminous stimulation is being diminished—either in consequence of frequent repetition at short intervals, or in consequence of the slow dying of the animal on an object-glass—the period of latency is very much prolonged. In this case the first effect of the flash is to cause retraction of the tentacles, to be followed immediately afterwards by a contraction of the bell. (This is also the case in other modes of stimulation of *feeble* specimens.) Lastly, it may be stated that when the marginal bodies of *Sarsia* are removed, the swimming-bell, although still able to contract spontaneously, no longer responds to luminous stimulation of any kind or degree. But if only one body be left *in situ*, or if the severed margin alone be experimented upon, the same unfailing response may be obtained to luminous stimulation as that which is obtained from the entire animal.

Although I have tested many of the Medusæ, I have obtained indications of response to luminous stimulation only in the case of one other species of the naked-eyed division.

This is a species which I have called *Tiaropsis polydiademata*, and the response which it gives to luminous stimulation is even more decided than is that which is given by *Sarsia*. In the opening paragraphs of my former paper, I described a peculiar spasmodic movement that is performed by *Staurophora laciniata* when subjected to marginal stimulation of any kind—a movement quite distinct from the ordinary locomotor contractions. A precisely similar movement is exhibited under similar circumstances by *Tiaropsis polydiademata*, and it is very interesting to observe that a sudden increase of light causes this peculiar spasm in this species quite as invariably and quite as decidedly as does any other kind of stimulation. Now in one remarkable particular this response to luminous stimulation on the part of *Tiaropsis polydiademata* differs from that given by *Sarsia tubulosa*; and the difference consists in the fact that while with *Sarsia* the period of latency is, so far as the eye can judge, as instantaneous in the case of response to luminous stimulation as it is in the case of response to any other kind of stimulation, such is far from being true with *Tiaropsis polydiademata*. The period of latency in the last-named species is, so far as the eye can judge, quite as instantaneous as it is in the case of *Sarsia*, when the stimulus employed is other than luminous; but in response to light the characteristic spasm does not take place till slightly more than a second has elapsed after the first occurrence of the stimulus. As this extraordinary difference in the latent period exhibited by the same animal towards different kinds of stimuli appeared to me a matter of considerable interest, I was led to reflect upon the probable cause of the difference. It occurred to me that the only respect in which luminous stimulation of the Medusæ differed from all the other modes of stimulation I had employed consisted in this—that, as proved by my previous experiments on *Sarsia*, which I repeated on *Tiaropsis*, luminous stimulation directly affected the central nervous tissues alone, while all the other modes of stimulation directly affected the contractile tissues. Now, as in *Tiaropsis polydiademata* luminous stimulation differed from all the other modes of stimulation in giving rise to an immensely longer period of latency, I seemed here to have an index of the difference between the rapidity of response to stimuli by the contractile and by the ganglionic tissues respectively. The next question, therefore, which presented itself was as to whether the enormous length of time occupied by the process of stimulation in the ganglia was due to any necessity on the part of the latter to accumulate the stimulating influence prior to originating a discharge, or to an immensely lengthened period of latent stimulation manifested by the ganglia under the influence of light. This is an interesting question, because if such a lengthened period of latent stimulation occurs in this case, it would stand in curious antithesis to the very short period of latent stimulation manifested by the contractile tissues of the same animal under other modes of irritation. To test these alternative hypotheses, I employed the very simple method of first allowing a continuous flood of light to fall suddenly on the Medusid, and then noting the time at which the responsive spasm first began. This time, as already stated, was slightly more than one second. I next allowed the animal to remain for a few minutes in the dark to recover shock, and, lastly, proceeded to throw in single flashes

of light of measured duration. I found that unless the flash of light was of slightly more than one second in its duration, no response was given. That is to say, the minimal duration of a flash required to produce a responsive spasm was just the same as the time during which a continuous flood of light required to operate in order to produce a similar spasm. From this, therefore, I conclude that the enormously long period of latent excitation in response to luminous stimuli was not, properly speaking, a period of latent excitation at all, but that it represented the time during which a certain summation of stimulating influence was taking place in the ganglia, which required somewhat more than a second to accumulate, and which then caused the ganglia to originate an abnormally powerful discharge.

With regard to luminous stimulation it is only necessary further to observe that responses were given equally well to direct sunlight, diffused daylight, and to light reflected from a mirror inclined at the polarizing angle. It must also be stated that responses are given to any of the luminous rays of the spectrum when these are employed separately, but that neither the non-luminous rays beyond the red, nor those beyond the violet, appear to exert the smallest degree of stimulating influence.

§ 5. *Electrical stimulation.* (A) *Latent periods and characters of the subsequent contractions.* (a) *Method.*—Under this heading I propose to treat at the same time of the period of latent stimulation and the manner in which this, as well as the responsive contractions, are modified by certain conditions. As *Aurelia aurita* is the only species on which I have experimented in this connexion, my remarks under this heading will be confined to it alone. The method by which I determined the latent period in the case of this species was as follows. A basin containing the Medusid was filled to its brim with sea-water, and placed close beside a cylinder which, while it lay in a horizontal position, could be rotated at a known rate. The *Aurelia** was placed with its concave aspect uppermost, and an inch or two below the surface of the water. The animal was held firmly in this position by means of a pair of compasses thrust through it and forced into a piece of wood which was sunk at the bottom of the basin. The legs of the compasses were provided with india-rubber sliders; so that by placing these under the Medusa, the latter might be kept at any elevation in the water which might be desired. The polypite and lithocysts were now removed, and also a segment of the disk. A light straw was then forced through the gelatinous substance of the umbrella in a radial direction, and close to the gap caused by the missing segment. The other, or free, end of this straw was firmly joined to a capillary glass rod, which was suitably bent to avoid contact with the rim of the basin and also to write on the smoked cylinder. If the straw was not itself sufficient to support the weight of the capillary rod, a small cross-piece of cork might easily be tied to it, so as to add to the floatation-power. A part of the excitable tissue was now raised

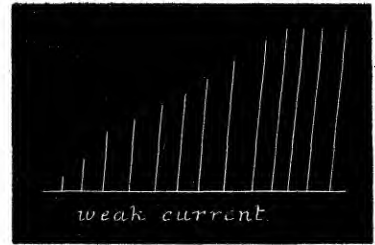
* It may here be stated that, in all the experiments on stimulation subsequently to be detailed, there is no difference to be observed between the behaviour of an entire swimming-organ deprived of its ganglia and that of a portion of any size which may be separated from it.

above the surface of the water by means of a disk of cork placed beneath it, and on the part of the tissue thus raised there were placed a pair of platinum electrodes. These electrodes proceeded from an electro-magnetic apparatus, which was arranged in such a way, that every time the current in it was opened or closed it gave an induction-shock and moved a lever at the same instant of time. This lever was therefore placed upon the cylinder immediately above the capillary glass writer which proceeded from the Medusa, care being taken to place the two writers in the same line parallel to the axis of the cylinder. Such being the arrangement, the cylinder was rotated, and thus two parallel lines were made upon it by the two writers. If the current was now closed, an induction-shock was thrown into the tissue at the same instant that the electro-magnet writer recorded the fact by altering its position on the cylinder. Again, as soon as the paralyzed Medusa responded to the induction-shock, the radii of the vacant segment were drawn apart, and in this way a curve was obtained by the other writer on the rotating cylinder. Now, by afterwards dropping a perpendicular line from the point at which the electro-magnet writer changed its position to the parallel line made by the other writer, and then measuring the distance between the point of contact and the point on the last-mentioned line at which the curve began, the period of latent stimulation was determined. A glance at figs. 2 & 3 will render this description clear to any one who is not already acquainted with the method, when it is stated that the upper line is a record of the movements of the electro-magnet writer, and the lower line that of the movements of the other writer. It will be observed that the point *a* in the upper line marks the point at which the induction-shock was thrown in; so that by first producing the perpendicular till it meets the lower line at *b*, and then measuring the distance between the point *b* and the point *c*, at which the curve in the lower line first begins, the latent period (*bc*) is determined—the time occupied by the rotation of the cylinder from *b* to *c* being known.

(*b*) *Summation of Stimuli*.—In this way I have been able to ascertain the period of latent stimulation in *Aurelia aurita* with accuracy. It must be stated at the outset, however, that this period is subject to great variations under certain varying conditions; so that we can only arrive at a just estimation of it by understanding the nature of the modifying causes. To take the simplest cause first, suppose that the paralyzed *Aurelia* has been left quiet for several minutes in sea-water at 45°, and that it is then stimulated by means of a single induction-shock. The responsive contraction will be comparatively feeble with a very long period of latency, viz. $\frac{5}{8}$ of a second. If another shock of the same intensity be thrown in as soon as the tissue has relaxed, a somewhat stronger contraction with a somewhat shorter latent period will be given. If the process is again repeated, the response will be still more powerful, with a still shorter period of latency; and so on for perhaps eight or ten stages, when the maximum force of contraction of which the tissue is capable will have been attained, while the period of latency will have been reduced to its minimum. This period is $\frac{2}{3}$ of a second, or, in some cases, slightly less.

Now we have here a very remarkable series of phenomena; and as it is a series which never fails to occur under the conditions named, I append tracings to give a better idea of the very marked and striking character of the results. The first tracing (fig. 1) is a record of the successive increments of the responses to successive induction-shocks of the same intensity thrown in at three seconds' intervals—the cylinder being stationary during each response, and rotated a short distance with the hand during each interval of repose.

Fig. 1.



The second tracing (figs. 2 & 3) is a record of the difference between the lengths of

Fig. 2.

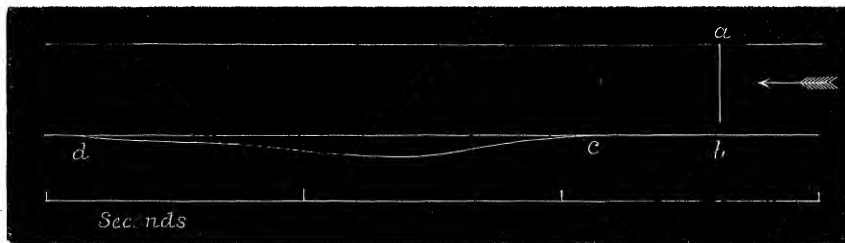
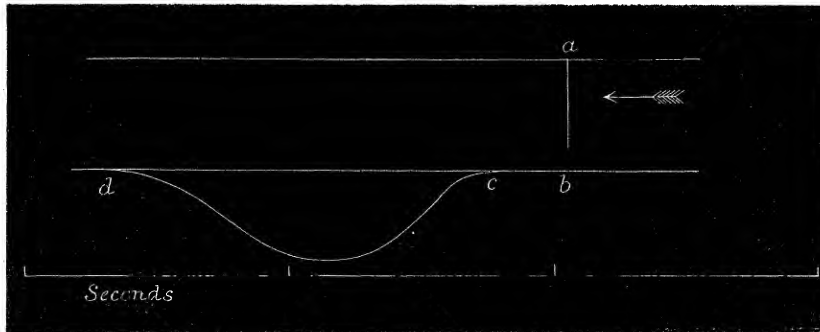


Fig. 3.



the latent period, and also between the strengths of the contraction, in the case, 1st, of the first of such a series of responses (fig. 2), and, 2nd, of the last of such a series (fig. 3). From these tracings it will be manifest, without further comment, how surprising is the effect of a series of stimuli, first in *arousing* the tissue, as it were, to increased *activity*, and second in developing a state of *expectancy*.

Those who are acquainted with Dr. BOWDITCH's investigation "concerning the irritability of the muscular fibres of the heart"*, cannot fail to be struck by the great simi-

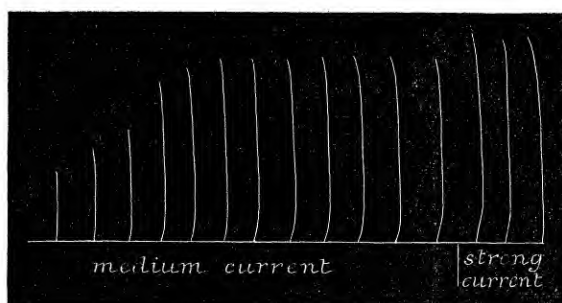
* LUDWIG, 'Arbeiten aus der physiologischen Anstalt zu Leipzig,' 1871, pp. 139-176. [It is further to be observed that a similar summation of stimuli has lately been observed to occur, in the case of reflex action, in the frog (Dr. STIRLING, 'Journal of Anat. and Physiol.' Jan. 1876) and in the excitable leaf of *Dionæa* (Dr. BURDON SANDERSON and Mr. PAGE, Proc. Roy. Soc. No. 177).—1877.]

larity of the first of the above tracings with those published in his paper. It will be remembered that he experimented on the physiologically severed apex of the heart, and therefore on a tissue which, in the absence of any active ganglionic element, resembles the paralyzed umbrella of *Aurelia*. His tracings were obtained in exactly the same way as my own, so that the fact of tissues separated from one another in the animal scale so widely as are the muscle-fibres of the heart and those of the Medusæ, nevertheless behaving towards stimulation in so peculiar and yet so similar a manner, is to my mind a fact of great interest. Dr. BOWDITCH does not appear to have determined the effect of what he conveniently terms the staircase action (from the appearance of the tracings to a staircase) upon the period of latent stimulation; but from the fact that in other respects the case of the heart and that of the Medusæ are so similar, there can be little doubt that in the former, as in the latter, the latent period will be found to be greatly influenced by a series of stimuli.

But although the case of the heart and the Medusæ are so wonderfully parallel in the particulars we are considering, there are one or two points of difference between them which must here be noted. In the case of *Aurelia*, after a staircase has been built up by means of a series of stimuli, if a pause of ten seconds be allowed to elapse and the stimulation be then again commenced, I find that the first response given is not quite of maximum intensity, but corresponds with perhaps the second or third step from the top of the previously completed staircase. Again, if a pause of fifteen seconds be allowed to elapse, the first step of the next staircase corresponds with the third or fourth step from the top of the standard one. If, again, a pause of half a minute be allowed to elapse, the first step of the next staircase will correspond in height only with the second or third step from the bottom of the first staircase. Lastly, if a whole minute be allowed to elapse between the maximum effect of one series of stimulations and the first stimulus of another series, it is observable that the tissue has, as it were, completely forgotten the occurrence of the previous series, so that the next staircase has to begin anew from the first step. Now Dr. BOWDITCH has found, in the case of the heart, that an interval of *five minutes* must be allowed to intervene between two series of stimuli before the effect of the first on the second is thus totally abolished; so that, returning to the metaphor first employed, we may say that the memory of the cardiac tissue is about five times as long as that of the medusoid tissue. But in the case of *exhausted* medusoid tissue the difference may be even greater than this; for in this case I have observed all memory to fade in the course of half a minute. There is one other point of difference between the heart and the Medusæ analogous to the one first stated. From Dr. BOWDITCH's tracings it appears that the maximum staircase effect is produced on the heart-apex when the successive shocks are thrown in at six seconds' intervals; whereas, in the case of the Medusæ, I found that the more rapidly the shocks are thrown in, the more marked is the beneficial influence of each contraction on its successor,—that is to say, up to the time when the interval between the successive shocks is not so short as to give rise to incipient tetanus by summation of contractions (when, of course, the

staircase effect is lost in that of tetanus), progressive shortening of the intervals between successive stimuli has the effect of progressively diminishing the number of steps in a staircase, and this by increasing the difference between the heights of the successive steps. Again, if a staircase has been built up by shocks thrown in at seconds' intervals, and the rate of stimulation be now suddenly changed to six seconds' intervals, the maximum level of the tracing that was obtained by the more rapidly succeeding shocks may be observed slightly to sink. This greater tolerance of the medusoid than of the cardiac tissue towards rapidity in the succession of stimuli is doubtless connected with the same differences in their constitution that leads to what I have called the shorter memory of the one than of the other. In this connexion it may also be stated that a staircase has more steps in it if caused by a weak than if caused by a strong current (compare figs. 1 & 4), and that if the strength of the current be suddenly increased after the

Fig. 4.



maximum level of a staircase has been attained by a feeble current, this level admits of being slightly raised (see fig. 4).

Lastly, the cases of the heart and of *Aurelia* appear not quite to coincide in one other particular; for I find that in *Aurelia* the staircase action is so pronounced, that a stimulus which at the bottom of a staircase is of less than minimal intensity, is able, at the top of a staircase, to give rise to a contraction of very nearly maximum intensity. That is to say, by employing an induction stimulus of slightly less than minimal intensity in relation to the original irritability of the tissue, no response is given to the first two or three shocks of a series; but at the third or fourth shock a slight response is given, and from that point onward the staircase is built up as usual. This was the case in the experiment of which fig. 1 is a record, no response having been given to the first two shocks. Now, as Dr. BOWDITCH does not state that a staircase may thus be built up by means of stimuli which at the beginning of the process are of less than minimal intensity, I infer that in the case of the heart this peculiarity is not observable.

With regard to this interesting staircase action, two questions naturally present themselves. In the first place, we are anxious to know whether the arousing effect which is so conspicuous in a staircase series is due to the occurrence of the previous *stimulations*, or to that of the previous *contractions*; and, in the next place, we should like to know whether, during the *natural* rhythm of the tissue, each con-

traction exerts a beneficial influence on its successor, analogous to that which occurs in the case of contractions that are due to *artificial* stimuli. Now both these questions admit of being answered by experiments on the Medusæ much more satisfactorily than they do by experiments on the heart—if, indeed, it is possible to answer them in the latter case at all. To answer the first of these questions, therefore, I built up a staircase in the ordinary way, and then suddenly transferred the electrodes to the opposite side of the disk from that on which they rested while constructing the staircase. On now throwing in another shock at this part of the contractile tissue so remote from the part previously irritated, the response resembled in all respects the one previously given, *i. e.* it was a maximum response. Similarly, if the electrodes were transferred in the way just described, not after the maximum effect had been attained, but at any point during the process of constructing a staircase, the response given to the next shock was of an intensity to make it rank as the next step in the staircase. Hence, shifting the position of the electrodes in no wise modifies the peculiar effect we are considering; and this fact conclusively proves that the effect is a general one pervading the whole mass of the contractile tissue, and not confined to the locality which is the immediate seat of stimulation. Nevertheless this fact does not tend to prove that the staircase-effect depends on the process of contraction as distinguished from the process of stimulation, because the wave of the former process must always precede that of the latter. But, on the other hand, in this connexion it is of the first importance to remember a fact recently stated, *viz.* that a current which at the beginning of a series of stimulations is of slightly less than minimal intensity, presently becomes of minimal, and eventually of much more than minimal intensity—a staircase being thus built up of which the first observable step (or contraction) only occurs in response to the second, third, or even fourth shock of the series. This fact, of course, clearly tends to show, or rather conclusively proves, that the staircase effect, at any rate at its commencement, depends on the process of stimulation as distinguished from that of contraction; for it is obvious that the latter process cannot play any part in thus constructing what we may term the invisible steps of a staircase.

To answer the second of the above questions, I placed an *Aurelia* with its concave surface uppermost, and removed seven of its lithocysts; I then observed the spontaneous discharge of the remaining one, and found it to be conspicuous enough—that after the occurrence of one of the natural pauses (if this were of sufficient duration) the first contraction was feeble, the next stronger, the next still stronger, and so on, till the maximum was attained. This natural staircase action admits of being very prettily shown in another way. If a tolerably large *Aurelia* is cut into a spiral strip of small width and great length, and if all the lithocysts are removed except one at one end of the strip, it may be observed that, after the occurrence of a natural pause, the first discharge only penetrates perhaps about a quarter of the length of the strip, the next discharge penetrates a little further, the next further, and so on, till finally the contractile waves pass from end to end. On now removing the ganglion, waiting a few

minutes, and then stimulating with successive induction-shocks, the same progressive penetration is observable as that which previously took place with the ganglionic stimulation. Lastly, the identity of natural and artificial staircase action may be placed beyond all doubt by an experiment in which the effects of induction-shocks and of ganglionic discharges are combined. To accomplish this, all the lithocysts save one are removed, and a staircase is then built up in the ordinary way by successive induction-shocks. It will now occasionally happen that the ganglion originates a discharge during the process of constructing the staircase; and when this does happen, it may invariably be observed that the contraction due to the natural stimulus is just of the proper intensity to take its place in the staircase which is being built up by the artificial stimuli, and this at whatever point the natural contraction happens to come in*.

Of course, in all these experiments with natural discharges, care must be taken to choose a lithocyst of a potency adapted to the object in view. This condition, before it is satisfied, often requires a number of trials to be made. The experiment with the spiral strip may prove particularly tedious in this respect, as it is difficult to obtain such a strip presenting the proper degree of resistance in relation to the terminal ganglion †.

* I may here observe that if an *Aurelia* with all its lithocysts removed happens, during the construction of a staircase by stimuli, to give a spontaneous contraction, this also ranks as the next step in the staircase, just in the same way as does a spontaneous contraction proceeding from a single remaining lithocyst. This proves that "secondary contractions" are not really, as Dr. EIMER describes them, more "feeble and inefficient" than primary ones; and that the only reason why they usually appear to be so is because they usually occur singly with a long interval between them, so that each secondary contraction usually corresponds with the first step of a staircase. But when, as sometimes happens, two or three secondary contractions follow one another at the rate observable in ordinary swimming, the second contraction is stronger than the first, and the third than the second, and so on, just as in the construction of a staircase by a single remaining lithocyst after the occurrence of a natural pause of adequate duration. It is almost needless to state that, as this effect of the summation of stimuli had not been observed at the time when Dr. EIMER published his paper, he is not to be accused of any inaccuracy in his observations because he described the "secondary contractions" as "feeble and inefficient."

† [As the present communication was originally accepted by the Royal Society, there here followed a lengthy subsection on "Artificial Rhythm." A condensed epitome of the main facts which were detailed in that subsection may be found in the already published abstract of this paper in the Proceedings of the Royal Society. But as the new theory of ganglionic action which it is the main object of this passage to disclose appears to me a theory of sufficient importance to demand its final publication in as complete a form as possible, I have sought and obtained the permission of the Royal Society to withdraw this subsection from the proof. And, as a further reason for postponing publication of the passage on "Artificial Rhythm," I may state that, as this paper is of undue length, it seemed to me desirable, if possible, to relegate a portion of it to my next paper; and I find that this subsection is the most suitable part temporarily to suppress, because the facts of which it treats form in themselves a connected body distinct from all the other facts which are detailed in the rest of this communication; so that while their omission from the present paper does not entail any further modification of the latter, they will admit of being introduced *en masse* in my next paper. When, therefore, I shall have completed the further experiments which in this connexion I have devised, I shall hope to communicate to the Royal Society, in a single connected series, all the facts and inferences which bear upon this subject.—1878.]

(c) *Temperature*.—Returning now to the period of latent stimulation in *Aurelia aurita*, we have seen how profoundly this period is modified by the staircase effect we have just been considering. We have next to contemplate the influence of temperature on the latent period and on the character of the contractions. But before stating my results, I may observe that in all my experiments in this connexion I changed the temperature of the Medusæ by drawing off the water in which they floated with a siphon, while at the same time I substituted water of a different temperature from that which I thus abstracted. In this way, without modifying any of the other conditions to which the animals were exposed, I was able to observe the effects of changing the temperature alone.

With regard to the effect of temperature on the latent period of stimulation, the following Table, setting forth the results of one among several experiments, explains itself.

Period of latent stimulation of the deganglionated tissues of *Aurelia aurita*
as affected by temperature.

Temperature of water (Fahr.).	Period of latent stimulation.
70°	$\frac{1}{5}$ second
50°	$\frac{1}{3}$ second
35°	$\frac{3}{5}$ second
20°	$\frac{1}{2}$ second

In the case of each observation several shocks were administered before the latent period was taken, in order to decrease this period to its minimum by the staircase action. When this is not done, the latent period at 20° may be as long as $1\frac{1}{5}$ second; but soon after this irritability disappears.

The extraordinary sluggishness of the latent period at very low temperatures is fully equalled by the no less extraordinary sluggishness of the contraction.

I may as well state here that in water at all temperatures, within the limits where responses to stimuli are given at all, the staircase action admits of being equally well produced. But in order to procure the maximum effect for any given temperature, the rate at which the successive stimuli are thrown in must be quicker in warm than in cold water; for in cold water the latent period and the subsequent contraction are both so prolonged, that summation of the contractions is produced by employing such intervals between the successive shocks as yield the maximum staircase effect in warmer water.

(B) *Tetanus*.—The allusion just made to summation of contractions leads us next to the subject of tetanus. As stated in my previous paper, some of the Medusæ, when subjected to faradaic stimulation, respond, not by a single prolonged tetanus, but by a flurried series of rapidly alternating contractions and relaxations. It must now be added that these remarks apply especially to *Sarsia*; for I find that in the case of *Aurelia* tolerably

strong faradization does cause a more or less well-pronounced tetanus. The continuity of the spasm is, indeed, often interrupted by momentary and partial relaxations. These interruptions are the more frequent the weaker the current; so that at a certain strength of the latter, the tetanus is of a wild and tumultuous nature; but with strong currents the spasm is tolerably uniform. That in all cases the tetanus is due to summation of contractions, may be very prettily shown by the following experiment. An *Aurelia* is cut into a spiral strip, and all its lithocysts are removed; single induction-shocks are then thrown in with a key at one end of the strip—every shock, of course, giving rise to a contractile wave. If these shocks are thrown in at a somewhat fast rate, two contractile waves may be made at the same time to course along the spiral strip one behind the other; but if the shocks are thrown in at a still faster rate, so as to diminish the distance between any two successive waves, a point soon arrives at which every wave overtakes its predecessor; and if several waves be thus made to coalesce, the whole strip becomes thrown into a state of persistent contraction.

In this way sustained tetanus, or single contractile waves, or any intermediate phase, may be instantly produced at pleasure. In such experiments, moreover, it is interesting to observe that, no matter how long the strip may be, whatever disturbances are set up at one end are faithfully transmitted to the other. For instance, if an *Aurelia* be cut into the longest possible strip with a remnant of the disk left attached at one end—as represented by Plate 33 in my previous paper—then all the peculiar time relations between successive contractions which are intentionally caused by the experimenter at one end of the strip, are afterwards accurately reproduced at the other end of the strip by the remainder of the disk. Now as this fact is observable however complex these time relations may be, and however rapidly the successive stimuli are thrown in, I think it is a point of some interest that these complicated relations among rapidly succeeding stimuli do not become blended during their passage along the thirty or forty inches of contractile tissue. The fact, of course, shows that the rate of transmission is so identical in the case of all the stimuli originated, that the sum of the effects of any series of stimuli is delivered at the distal end of the strip with all its constituent parts as distinct from one another as they were at starting from the proximal end of the strip.

IV. SECTION.

In this division I shall treat of all the evidence I have been able to collect regarding the distribution of nerves and the physiological character of the contractile tissues in the various species of Medusæ which have this year fallen within my observation. By the word “nerves” here I mean certain physiologically differentiated tracts of tissue which either stimulation or section prove to perform the function of conveying impressions to a distance; and by “physiological character of the contractile tissues” I mean the character of these tissues in respect of the degree in which the nervous element shows itself to be physiologically differentiated from the muscular element.

§ 1. *Distribution of Nerves in Sarsia.* (A) *Reflex Action.*—The occurrence of reflex

action in *Sarsia* is of a very marked and unmistakable character. I may begin by stating that when any part of the internal surface of the bell is irritated, the polypite responds; but as there is no evidence of ganglia occurring in the polypite, this cannot properly be regarded as a case of reflex action. But, now, the converse of the above statement is likewise true, viz. that when any part of the polypite is irritated, the bell responds; and it is in this that the unequivocal evidence of reflex action consists. Of course the objection at once arises, if response by the polypite to irritation of the bell is explained by the simple supposition of there being a continuous or common excitability pervading these organs, why may not the converse case be explained by the same supposition? But this objection is met by a fact that makes an essential difference between the two cases, viz. that while the sympathy of the polypite with the bell is not in the least impaired by removing the marginal ganglia of the latter, the sympathy of the bell with the polypite is by this operation entirely destroyed.



We have thus very excellent demonstration of the occurrence of reflex action in the Medusæ; and as this is such an admirable instance of it, I shall describe it a little more in detail. Suppose the experimenter to have chosen a vigorous specimen of *Sarsia* with its polypite well retracted, and suppose him to wait for the occurrence of one of the natural pauses in the swimming-motions; if he then suddenly seizes the end of the polypite with a pair of forceps, taking care not to touch any part of the bell, the polypite is instantly retracted even further than it was before, and immediately afterwards the tentacles are drawn up while the bell begins to make violent efforts to escape. But if the experimenter chooses a specimen having its polypite somewhat relaxed, and, after seizing the free end of this organ, follows it up with the forceps during its retreat, he may observe, if he has been dexterous enough not to allow the slightest pull to occur at the point of suspension of the polypite, that the bell does not respond to the stimulus however severe this may have been. By repeating this experiment a number of times, it becomes evident that the reflex action occurs, not between the marginal ganglia and every part of the polypite, but between the marginal ganglia and the point of the bell from which the polypite is suspended. In other words, the marginal ganglia do not respond to any amount of disturbance that may be set up in the polypite itself, provided the contraction of this organ does not cause it to pull upon the point of its attachment with the bell. Now the high degree of sensitiveness shown by the ganglia to the smallest degree of such traction is quite as remarkable as is their lack of sensitiveness to disturbances going on in the polypite*. Consequently

* When a specimen of *Sarsia* is taken out of the water, laid on an object-glass, slit open along one side, and spread out flat with its inner surface uppermost, and then has its polypite turned back as represented in the figure on p. 697, it may be observed that the bell often responds to irritations of the polypite, even though care be taken to release the latter from the forceps before it is allowed to pull on its point of suspension. This may possibly be due to the fact of the polypite meeting with some friction on the glass during its process of retraction, which friction must cause it to pull very slightly on its point of suspension. At any rate, if it is due to nervous connexions between the substance of the polypite and the marginal ganglia, the conducting-power, as estimated by the response of the distant tissue, is much less in the direction we are now considering than it is in the converse

we have in this a very conclusive proof of the truly reflex character of the action we are considering; for after the removal of the marginal ganglia, the mutilated nectocalyx, although it remains most keenly sensitive to the gentlest stimulation applied to its own irritable tissues, will allow itself to be dragged through the water as rapidly as possible by means of the polypite without giving a single contraction. But, in this experiment, if the smallest atom of marginal tissue be left *in situ*, the ganglion cell or cells contained in that atom will suffice to preserve the reflex action. In this case, however, the responses are neither so ready nor so sure as they are when a larger amount of ganglionic matter is concerned in the process.

(B) *Nervous connexions between the Tentacles of Sarsia*.—When one of the four tentacles of *Sarsia* is very gently irritated, it alone contracts. If the irritation be slightly stronger, all the four tentacles, and likewise the polypite, contract. If one of the four tentacles be irritated still more strongly, the bell responds with one or more locomotor contractions. If in the latter case the stimulus be not too strong, or, better still, if the specimen operated on be in a non-vigorous or in a partly anæsthesiated state, it may be observed that a short interval elapses between the response of the tentacles and that of the bell. Lastly, the polypite is much more sensitive to a stimulus applied to a tentacle, or to one of the marginal bodies, than it is to a stimulus applied at any other part of the nectocalyx*.

These facts clearly point to the inference that nervous connexions unite the tentacles with one another and also with the polypite—or, perhaps more precisely, that each marginal body acts as a coordinating centre between nerves proceeding from it in four directions, viz. to the attached tentacle, to the margin on either side, and to the polypite. This, it will be observed, is the distribution which HÆCKEL describes as occurring in *Geryonia*, and SCHULTZ as occurring in *Sarsia*†. It is further the distribution to which my explorations by stimulus of last year would certainly point. But, in order to test the matter still more thoroughly, I tried the effects of section in destroying the

direction, which is to be immediately considered in the text (B). And as it seems probable that in such a simple case as this the same nerves would serve to convey impressions in both directions, perhaps the most judicious view to take of the difference between the degree of sensitiveness displayed by the polypite when a tentacle is injured, and that displayed by the tentacles when the polypite is injured, is to suppose that in the former case a feeble ganglionic discharge is added to the stimulus, which discharge would of course be absent in the latter case.

* These facts were partly ascertained by the method of experimentation described in the last footnote. It must here be added that in conducting such experiments the greatest care must be taken not to agitate the drops of water in which the animal is contained. The disturbance caused by capillarity on introducing the needle-point into these few drops of water is sufficient to cause the tentacles and polypite to contract, even though they be a long way off. I therefore used two object-glasses separated by a small interval, so as to break the continuity of the water between the point of irritation and that of the tissue whose physiological connexions with such point I wished to ascertain.

† ‘Ueber den Bau von *Syncoryne Sarsia* und der zugehörigen Medusa *Sarsia tubulosa*,’ by Dr. F. E. SCHULTZ (Leipzig, 1873). My attention has been directed by my friend Professor LANKESTER to this admirable little monograph on *Sarsia*. The histological elements to which the author ascribes a nervous function are quite familiar to me, and I think that at any rate some of his views with regard to them are probably correct.

physiological relations which I have just described. These effects, in the case of the tentacles, were sufficiently precise. A minute radial cut introduced between each pair of adjacent marginal bodies—there being thus four such cuts in all—as a rule completely destroyed the physiological connexion between the tentacles; or if, as in some cases, such connexions were not completely destroyed by this operation, they were at least conspicuously impaired. If only three marginal cuts were introduced, the sympathy between those two adjacent tentacles between which no cut was made continued unimpaired, while the sympathy between them and the other tentacles was either destroyed or greatly impaired. In all cases where the sympathy between tentacles was not wholly destroyed, but merely impaired, the impairment showed itself in this way. Whereas before the introduction of the radial cuts the slightest nip of one tentacle caused an instantaneous response on the part of all the tentacles, after the operation such a stimulus applied to one tentacle would perhaps cause no effect at all on the other tentacles, though on gently *pulling* one of the tentacles the others would retract at the same time as the bell, in response to this severe stimulus, would give a locomotor contraction. And as, before mutilation, the tentacles may be observed to respond to such a stimulus an exceedingly short time *before* the bell, I conclude that, after mutilation, the *time* required for the stimulus to pass round the margin from one tentacle to the others is increased. Hence the cases in which the sympathy between the tentacles is not wholly destroyed by the four minute radial cuts are, I think, to be regarded as cases in which those quadrants of the margin which have been physiologically separated from beneath nevertheless continued united to each other from above. And this junction I conceive to be effected by means of nerve-loops which are composed of smaller fibres than those of the margin, and which may be supposed to join the artificial quadrants of the margin by traversing the muscular tissue of the bell in all directions above the level that is reached by the short radial cuts*.

(C) *Nervous connexion between the Tentacles and the Polypite of Sarsia*.—Having obtained such definite results in the case of the tentacles, I expected to do the same in the case of the polypite. Accordingly I began by severing one of the nutrient tubes across its diameter, and then nipping the tentacle at the end of that tube. The polypite responded as before. Knowing from my previous experiments that the stimulus escaped round the margin of the nectocalyx, I thought it probable that the reason why the polypite now responded was because the stimulus found its way up the three unsevered tubes†. I therefore divided all the four nutrient tubes; but the polypite still continued to respond to a stimulus applied to any of the tentacles. Next, in the same specimen, I made two radial cuts, one on each side of a marginal body, and then irritated the tentacle attached to that body; the polypite contracted as before. Lastly, I treated the other three

* In the foregoing and subsequent descriptions, by “short radial cuts” I mean cuts which are only just long enough to sever the tissues of the extreme margin.

† For the sake of brevity I speak of the nutrient tubes as themselves the excitable tracts, although anatomically, no doubt, these tracts are distinct from the nutrient tubes.

bodies in the same way, and the polypite still contracted when I irritated any one of the four tentacles.

Now, as these experiments were repeated on a number of specimens—the radial tubes being in some cases divided at the base and in others at the apex of the cone—and as the experiments always yielded the same result, I cannot doubt that the nervous connexions between the margin and the polypite are in no wise restricted to the course of the nutrient tubes.

(D) *Nervous connexion between the Nectocalyx and the Polypite of Sarsia.*—The polypite of *Sarsia* often shows itself more sensitive than does the nectocalyx to stimuli applied to the latter. Moreover, as already stated, the polypite of *Sarsia* is much more sensitive to stimuli applied to a tentacle or to a marginal body of the nectocalyx than to stimuli applied at any other part of that organ. As regards the general surface of the irritable tissue of the nectocalyx, the polypite is more sensitive to stimuli applied at some parts than it is to stimuli applied at other parts; but in different specimens there is no constancy as to the position occupied by these excitable tracts. I think, however, that, as a general rule, stimulation of the parts of the bell nearest to the insertion of the polypite causes the latter to respond more readily than does stimulation of the parts more distant. Over all parts of the bell, however, during such explorations, sudden variations in the responses of the polypite are observable according as the electrodes are shifted a millimetre or less one way or the other; in some cases, indeed, even a few hair-breadths will make all the difference between an active response and no response. Similarly with mechanical stimulation.

From these explorations, therefore, it would seem that the polypite of *Sarsia* is in very intimate communication with the nectocalyx, and especially with the marginal bodies, by means of a nervous plexus pervading the excitable tissues of the latter, but that the principal nervous tracts by which this communication is effected are not constant as to their position in different individuals.

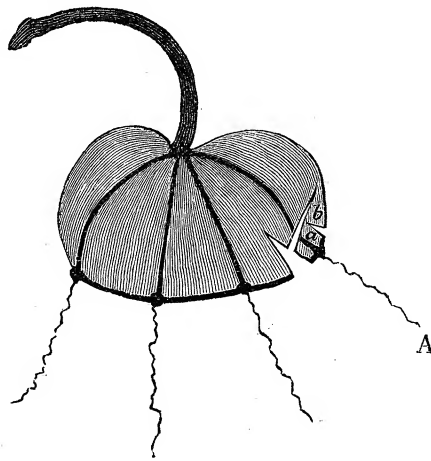
(E) *Character of the Excitable Tissues of Sarsia.*—It will be remembered that in my former paper I described several experiments which were designed to test the amount of section that the excitable tissues of the Medusæ would tolerate without suffering loss of their “physiological continuity.” This term, as previously used by Dr. FOSTER, implies such a condition of excitable tissue that its various parts are in physiological connexion with one another, whether by means of contractile elements (protoplasm, muscle) or conductile elements (“lines of discharge,” nerves). Therefore, in my last paper, I employed this term to designate such a condition on the part of contractile tissues as admits of an uninterrupted passage along their substance of what I called “contractile waves.” But having in the present paper an important distinction to draw, I must discard the *generic* term “*physiological* continuity,” and substitute for it two *specific* terms, viz. “*contractional* continuity” and “*excitational* continuity.” By “*contractional* continuity” I shall wish to be understood such a condition of contractile tissue as admits of the uninterrupted passage of contractile waves; while by “*excitational* continuity” I shall wish to be understood such a condition of the contractile tissues as

admits of one part responding to stimuli applied at another part, *whether or not contractile waves are able to pass along the intervening parts**.

With this distinction clearly understood, I shall now proceed to describe some experiments which were devised in order to test the amount of section that the excitable tissues of *Sarsia* would endure without suffering loss of their excitational continuity. The experiments detailed in the foregoing subsections were really experiments of this kind; but such experiments derive a special interest when conducted on the general contractile-sheet of the Medusæ. They do so because, as we have already seen, there is here decided indication of a nervous plexus; and it will be remembered that some of the most interesting questions with which my last paper was concerned, and which it left unanswered, were, first as to the presence of such a nerve-plexus, and next as to the extent in which, if present, it was differentiated from the muscular element.

Now, as stated in my former paper, the contractile tissues of *Sarsia* will endure very severe forms of radial and spiral section without suffering loss of their contractional continuity; but I find that, as a rule, their tolerance is not nearly so great as regards the maintenance of their excitational continuity. To save space I will only give one average

Fig. 6.



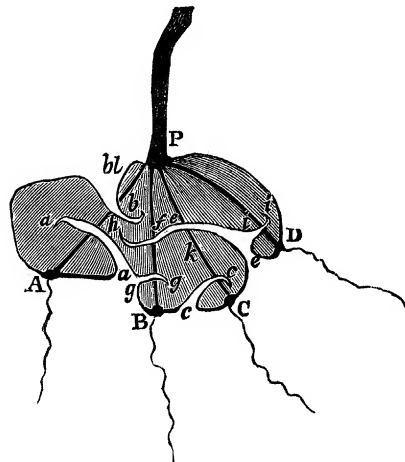
case. The figure (fig. 7) represents a specimen of *Sarsia* spread flat on an object-glass after having been slit open along one side. The experiment consisted in determining the

* I choose these terms, because they are the only ones I can think of to express the meaning I wish to convey. There is evidently a broad distinction—and a very important one for the purposes of this paper—between the passage of a contractile wave from the point of stimulation A to the point of destination B, and the passage of an unseen molecular wave from A to B, the existence of which is only rendered apparent by the response at B to the stimulus applied at A. And as it is further evident that this distinction has reference to the most fundamental quality wherein the function of nerve is distinguished from that of muscle, viz. the power of setting up responsive contractions at a distance from the seat of irritation, it will be understood that by the term “excitational continuity” I intend to denote the first indications we can perceive in the animal kingdom of the distinguishing function of nerve-tissue. The terms which I have employed are not to be found in our standard dictionaries; but their introduction is justified by the analogy of such words as “emotional,” “sensational,” &c.

severity of section which the nervous connexions between the nectocalyx and the polypite would endure without being wholly destroyed; and, as these connexions are always most intimate between the polypite and the marginal bodies or the tentacles, the points chosen for irritation were the latter. If the reader will endeavour to imagine all the curved sections represented in fig. 7 to be absent, as they are in the left-hand portion of fig. 6, he will understand that on irritating the tentacle marked A, the polypite P immediately responded. On now introducing the incision marked *aa*, the polypite still continued its response to stimuli applied at A; but on adding the cut marked *bb*, such responses ceased. The connexions, however, between C and P were of course still intact, and they were not destroyed by introducing the cut *cc*; but they were destroyed on adding the cut *ee*. Nevertheless, on now irritating the divided nutrient tube in any point of its division *k*, the polypite still responded; accordingly the cut *ee* was continued to *f*, and this had the effect of destroying the connexions between *k* and P. Excitational continuity still subsisted between B and P; therefore the cut *gg* was introduced: responses still being given, the cut *eeff* was produced to *h*, when the connexions between P and B were destroyed. Lastly, on irritating D, P responded; but, on introducing the cut *ii*, responses ceased.

From this instance it will be seen that, even in the same individual, there are considerable differences in the degree of tolerance manifested towards section by different homologous parts; but a number of experiments of this kind have satisfied me that in *Sarsia* the loss of excitational continuity between the polypite and bell generally supervenes much earlier than does that of contractional continuity between different parts of the bell. The preceding sketch, fig. 6, represents the most extreme instance

Fig. 7.



of tolerance as regards excitational continuity that I have observed in the case of *Sarsia*. In this instance the polypite continued to respond to stimuli applied at the tentacle marked A after the line of junction-tissue marked *ab* had been reduced to the thickness of one fortieth of an inch.

(F) *Stimulation of the Convex Surface of the Nectocalyx of Sarsia*.—I have this year

tried the effects of stimulating the convex, or external, surface of *Sarsia*, in consequence of its having been suggested to me that, as this is the surface which is naturally the most liable to come in contact with foreign bodies during the natural swimming-motions of the animal, it is to be expected that this part of the animal should receive a nerve-supply from the marginal ganglia. But although this is what we might reasonably expect to be the case, as a matter of fact it is not so. Even strong faradaic stimulation applied to any part of the external surface of the nectocalyx fails to produce the slightest response, provided the current employed is not so strong as to cause escape into the internal surface. That the responses are due to such an escape of the current when over-strong currents are used, may be proved by using weaker currents and progressively pushing the needle-point terminals further and further into the gelatinous substance of the nectocalyx. According to the strength of the current employed, a point will sooner or later be reached at which the escape finds its way to the internal surface, and thereupon causes the bell to contract.

In these experiments it is desirable to use electrical or chemical stimulation, because, when the animal is suspended in water, it is impossible to stimulate the external surface of the bell mechanically without causing the whole animal to move slightly through the water, and to any such disturbance the marginal ganglia are wonderfully sensitive. If, however, it is desired to give mechanical stimuli a fair trial in this connexion, the experiment may be conducted by placing a vigorous specimen of *Sarsia* on a grooved object-glass, when it may be observed that on touching the apex of the bell with a needle no response is given, unless the touch is strong enough to cause the whole animal to slide along the glass. Similarly, if one side of the bell be touched, no response is given until the pressure exerted is sufficiently great to force the subjacent *internal* surface against that of the opposite side.

I have here chosen *Sarsia* for special description, because it is the most active of the Medusæ which have come under my observation. In the case of the covered-eyed Medusæ, no such precautions as those which I have just described are necessary; for the massive nature of their swimming-organs gives them a considerable amount of inertia as they float in the water, and pretty severe mechanical stimulation may be applied to their external surfaces without causing any displacement of the animal.

These experiments, then, conclusively prove that, in the case of all the Medusæ I have examined, irritability of the swimming-organ is exclusively confined to the thin layer of contractile tissue which everywhere constitutes the internal surface of that organ.

§ 2. *Distribution of Nerves in Tiaropsis indicans.* (A) *Reflex action* (?).—We have seen that in *Sarsia* reflex action obtains between the polypite and the bell; we shall now see that in *Tiaropsis indicans* something resembling reflex action obtains between the bell and the polypite. The last-named species is a new one which I have described elsewhere*, and I have called it "*indicans*" from a highly interesting and important peculiarity of function that is manifested by its polypite. The Medusa in question

* "New Species, Varieties, and Monstrous Forms of Medusæ," Journ. Linn. Soc., Zool. vol. xii. p. 524.

measures about $1\frac{1}{2}$ inch in diameter, and is provided with a polypite of unusual proportional size, its length being about $\frac{5}{8}$ of an inch and its thickness being also considerable. Now if any part of the nectocalyx be irritated, the following series of phenomena takes place. Shortly after the application of the stimulus, the large polypite suddenly contracts, the appearance presented being that of an exceedingly rapid crouching movement. The crouching attitude in which this movement terminates continues for one or two seconds, after which the organ begins gradually to resume its former dimensions. Concurrently with these movements on the part of the polypite, the portion of the nectocalyx which was irritated has been gradually bending inwards towards the polypite, and by the time that the latter has again become fully extended, the portion of the nectocalyx in question has bended inwards as far as it is able. The polypite now begins to deflect itself towards the bent-in portion of the nectocalyx; and this deflection continuing with a somewhat rapid motion, the extremity of the polypite is eventually brought, with unerring precision, to meet the in-bent portion of the nectocalyx. I here introduce a drawing of twice life-size to render a better idea of this *pointing* action by the polypite to a seat of irritation located in the bell (see Plate 30. fig. 1). It must further be stated that in the un mutilated animal such action is quite invariable, the tapered extremity of the polypite never failing to be placed on the exact spot in the nectocalyx where the stimulation is being, or had previously been, applied. Moreover, if the experimenter irritates one point of the nectocalyx, with a needle or a fine pair of forceps for instance, and while the polypite is applied to that point he irritates another point, then the polypite will leave the first point and move over to the second. In this way the polypite may be made to indicate successively any number of points of irritation; and it is interesting to observe that when, after such a series of irritations, the animal is left to itself, the polypite will subsequently continue for a considerable time to visit first one and then another of the points which have been irritated. In such cases it usually dwells longest and most frequently on those points which have been irritated most severely.

I think the object of these movements is probably that of stinging the offending body by means of the urticating cells with which the extremity of the polypite is armed. But, be the object what it may, the fact of these movements occurring is a highly important one in connexion with our study of the distribution of nerves in Medusæ; and the first point to be made out with regard to these movements is clearly as to whether or not they are of a truly reflex character. Accordingly I first tried cutting off the margin and then irritating the muscular tissue of the bell; the movements in question were performed exactly as before. These movements, therefore, supply an additional instance of the rule laid down in my former paper, viz.: "Every Medusa, when its centres of spontaneity have been removed, responds to a single stimulation by once performing that action which it would have performed in response to that stimulation had its centres of spontaneity still been intact." Now the fact of this rule holding good in this case opens up an interesting subject for our contemplation. It

will be observed that, so far as the movements in question are themselves concerned, they are undistinguishable from an ordinary reflex act—such, for instance, as we have observed to occur in *Sarsia*. But we are accustomed to hear that for the occurrence of a truly reflex act, the presence of ganglionic or central nerve-matter is requisite. Yet in the case before us we have exceedingly precise action of an apparently reflex kind, which is nevertheless quite independent of the only ganglia that can be shown to occur in the organism. In view of this fact, therefore, I was led to think it probable that the reflex centres I was in search of might be seated in the polypite. Accordingly I cut off the polypite, and tried stimulating its own substance directly. I found, however, that no matter how small a portion of this organ I used, and no matter from what part of the organ I cut it, this portion would do its best to bend over to the side which I irritated. Similarly, no matter how short a stump of the polypite I left in connexion with the nectocalyx, on irritating any part of the latter, the stump of the polypite would deflect itself towards that part of the bell, although of course, from its short length, it was unable to reach it. Hence there can be no doubt that every portion of the polypite—down, at least, to the size which is compatible with conducting these experiments—is independently endowed with the capacity of very precisely localizing a point of irritation which is seated either in its own substance or in that of the bell*.

We have here, then, a curious fact, and one which it will be well to bear in mind during our subsequent endeavours to frame some sort of a conception regarding the nature of these primitive nervous tissues. The localizing function which is so very efficiently performed by the polypite of this Medusa, and which, if any thing resembling it occurred in the higher animals, would certainly have definite ganglionic centres for its structural correlative, is here shared equally by every part of the exceedingly tenuous contractile tissue that forms the outer surface of the organ. I am not aware that such a diffusion of ganglionic function has as yet been actually proved to occur in the animal kingdom; but I can scarcely doubt that future investigation will show such a state of things to be of common occurrence among the lower members of that kingdom†.

* It must here be added that the same remark may be made with reference to the nectocalyx; for however small a part of this organ is excised, it will bend inwards on being irritated. This case, however, is not nearly so remarkable as is that of the polypite, because, in the first place, there is no choice of *direction* to be exercised, and, in the next place, this bending inward of the nectocalyx upon irritation occurs more or less in the case of all the species of this genus, and is no doubt identical with the spasmodic movement exhibited under similar circumstances by *Staurophora luciniata*, to which attention was directed in my last paper, and which will form the subject of the next section of the present one. The only respect in which, so far as I can see, the inflexion of the seat of irritation in *Tiaropsis indicans* is distinguishable from the spasm of some other species of *Tiaropsis* and of *Staurophora* consists in its being of a local instead of a general character.

† The only case I know which rests on direct observation, and which is at all parallel to the one above described, is the case of the tentacles of *Drosera*. Mr. DARWIN found, when he cut off the apical gland of one of these tentacles together with a small portion of the apex, that the tentacle thus mutilated would no longer respond to stimuli applied directly to itself. Thus far the case differs from that of the polypite of *Tiaropsis indicans*, and in respect of localization of coordinating function resembles that of ganglionic action. But Mr. DARWIN

(B) *Nervous connexions between the Nectocalyx and Polypite of Tiaropsis indicans*.—

(a) In the last subsection we have virtually seen that if we have regard to *function* alone the localizing action of the polypite of *Tiaropsis indicans* may properly be termed a reflex action, but that if we have regard to the *structure* or mechanism by which this action is performed we cannot properly so term it. We have virtually seen this, because we have seen that at least one element essential to the mechanism whereby reflex action is effected—the element, namely, of a definite localized ganglion—is here absent. The next question, therefore, which arises is, as to whether the other elements which are usually considered essential to the performance of reflex action are likewise absent—the elements, namely, of afferent and efferent nerves. Now I felt so persuaded of the difficulty of answering this question by means of histological research, that hitherto I have postponed the latter, and, giving priority to the method of section, I obtained the most definite results with regard to function which it is possible for this or for any other method to yield.

(b) Bearing in mind that in an unmutilated *Tiaropsis indicans* the polypite invariably localizes with the utmost precision any minute point of irritation situated in the bell, the significance of the following fact is unmistakable, viz. that when a cut is introduced between the base of the polypite and the point of irritation in the bell, the localizing power of the former as regards that point in the latter is wholly destroyed. For instance, if such a cut as that represented at *a* (see Plate 30. fig. 1) be made in the nectocalyx of this Medusa, the polypite will no longer be able to localize the seat of a stimulus applied below that cut, as, for instance, at *b*. Now, having tried this experiment a number of times and having always obtained the same result, I conclude that the nervous connexions between the bell and the polypite which render possible the localizing action of the latter, are connexions the functions of which are intensely specialized, and the distribution of which is radial.

(c) So far, then, we have highly satisfactory evidence of tissue tracts performing the function of afferent nerves. But another point of great interest arises. Although in the experiment just described the polypite is no longer able to *localize* the seat of stimulation in the bell, it nevertheless continues able to perceive, so to speak, that

also found that such a “headless tentacle” continued to be influenced by stimuli applied to the glands of neighbouring tentacles—the headless one in that case bending over in whatever direction it was needful for it to bend in order to approach the seat of stimulation. This shows that the analogue of ganglionic function must here be situated in at least more than one part of a tentacle; and I think it is not improbable that, if trials were expressly made, this function would be found to be diffused throughout the whole tentacle.

Of course in here using the term “analogue of ganglionic function,” I do not commit myself to supposing that any thing resembling ganglionic *structure* occurs in any part of *Drosera*. On the contrary, I have here alluded to the case of *Drosera* just because it is a case in which we cannot expect to meet with any such structure, and therefore a case confirmatory of the views to which, I think, my own investigations point—viz. that before the functions of ganglion are localized in any characteristic histological structure, they occur in a more or less diffused manner in primitive contractile tissues. But as yet I have not had time to give the histology of *Tiaropsis indicans* the attention which it deserves.

stimulation is being applied in the bell *somewhere*; for every time any portion of tissue below the cut *a* is irritated, the polypite actively dodges about from one part of the bell to another, applying its extremity now to this place and now to that one, as if seeking in vain for the offending body. If the stimulation is persistent, the polypite will every now and then pause for a few seconds, as if trying to decide from which direction the stimulation is proceeding, and will then suddenly move over and apply its extremity, perhaps, to the point that is opposite to the one which it is endeavouring to find. It will then suddenly leave this point and try another, and then another and another, and so on, as long as the stimulation is continued. Moreover, it is important to observe that there are *gradations* between the ability of the polypite to localize correctly and its inability to localize at all—these gradations being determined by the circumferential distance from the end of the cut at which the stimulus is applied, and also by the radial distance between the cut and the point of stimulation. For instance, in figure 1 suppose a cut AB, $\frac{1}{4}$ of an inch long, to be made pretty close to the margin and concentric with it, then a stimulus applied at the point *c*, just below the middle point of AB, would have the effect of making the polypite move about to various parts of the bell, without being able in the least degree to localize the seat of irritation. But if the stimulus be applied at *d*, the polypite will probably be so far able to localize the seat of irritation as to confine its movements, in its search for the offending body, to perhaps the *quadrant* of the bell in which the stimulation is being applied. If the stimulation be now applied at *e*, the localization on the part of the polypite will be still more accurate; and if applied at *f* (that is, *almost* beneath one end of the cut AB) the polypite may succeed in localizing quite correctly.

These facts may also be well brought out by another mode of section, which is described in my former paper as “cutting round a greater or less extent of the marginal tissue, leaving one end of the resulting strip free, and the other end attached *in situ*.” If this form of section be practised on *Tiaropsis indicans*, as represented at *g, k* in the figure, it may always be observed that irritation of a distant point in the marginal strip, such as *g* or *h*, causes the polypite to move in various directions, without any special reference to that part of the bell which the irritated point of the marginal strip would occupy if *in situ*. But if the stimulation be applied only one or two millims. from the point of attachment of the marginal strip, as at *i*, the polypite will confine its localizing motions to perhaps the proper quadrant of the bell; and if the stimulus be applied still nearer to the attachment of the severed strip, as at *j*, the localizing motions of the polypite may become quite accurate.

Again, with regard to *radial* distance, if the cut AB in the figure were situated higher up in the bell, as at A'B', and the arc, *c, d, e, f*, of the margin irritated as before, the polypite would be able to localize better than if, as before, the radial distance between AB and *c, d, e, f* were less. The greater this radial distance, the better would be the localizing power of the polypite; so that, for instance, if the cut A'B' were situated nearly at the base of the polypite, the latter organ might be able to localize correctly

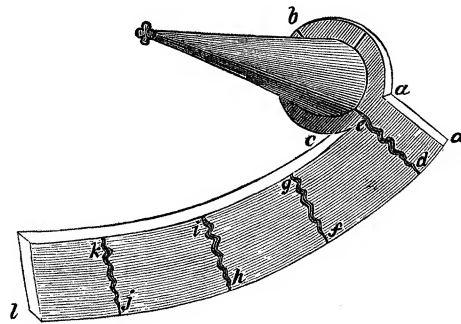
a stimulus applied, not only as before at *f*, but also at *e* or *d*. In such comparative experiments, however, it is to be understood that the higher up in the bell a cut is placed, the shorter it must be; for a fair comparison requires that the two ends of the cut shall always touch the same two radii of the nectocalyx. Still, if the cut is only a very short one (say 1 or 2 millims. long), this consideration need not practically be taken into account; for such a cut, if situated just above the margin, as represented at *a*, will have the effect of destroying the localizing power of the polypite as regards the corresponding arc of the margin; but if situated high up in the bell, even though its length be still the same, it will not have this effect.

From all this, then, we have seen that the connexions which render possible the *accurate* localizing functions of the polypite are almost, though not quite, exclusively radial. We have also seen that between accurate localization and mere random movements on the part of the polypite there are numerous gradations—the degree of decline from one to the other depending on the topographical relations between the point of stimulation and the end of the section (the section being of the form represented by AB in the figure). These relations, as we have seen, are the more favourable to correct localization, (*a*) the greater the radial distance between the point of stimulation and the end of the section; and (*b*) the less the circumferential distance between the point of stimulation and the radius let fall from the end of the section. But we have seen that the limits, as regards severity of section, within which these gradations of localizing ability occur are exceedingly restricted—a cut of only a few millims. in length, even though situated at the greatest radial distance possible, being sufficient to destroy all localizing power of the polypite as regards the middle point of the corresponding arc of the margin, and a stimulus applied only a few millims. from the attached end of a severed marginal strip entirely failing to cause localizing action of the polypite. Lastly, we have seen that even after all localizing action of the polypite has been completely destroyed by section of the kinds described, this organ nevertheless continues actively, though ineffectually, to search for the seat of irritation.

(*d*) The last-mentioned fact shows that after excitational continuity of a higher order has been destroyed, excitational continuity of a lower order nevertheless persists. Or, to state the case in other words, the fact in question shows that after severance of the almost exclusively radial connexions between the bell and the polypite by which the perfect or impaired localizing function of the latter is rendered possible, other connexions between these organs remain which are not in any wise radial. I therefore next tested the degree in which these non-radial connexions might be cut without causing destruction of that excitational continuity of a lower order which it is their function to maintain. It will here suffice to record one mode of section which has yielded important results. A glance at the accompanying figure (8) will show the manner in which the Medusa is prepared. The margin having been removed (in order to prevent possible conduction by the marginal nerve-fibre), a single deep radial cut (*aa*) is first made, and then a circumferential cut (*a, b, c*) is carried nearly all the way

round the base of the polypite. In this way the nectocalyx, deprived of its margin, is converted into a continuous band of tissue, one of the ends of which supports the polypite. Now it is obvious that this mode of section must be very trying to nervous connexions of any kind subsisting between the bell and the polypite. Nevertheless, in many cases, irritating any part of the band al has the effect of causing the polypite to perform the active random motions previously described. In such cases, however, it is observable that the further away from the polypite the stimulus is applied, the less active is the response of this organ. In very many instances, indeed, the polypite altogether fails to respond to stimuli applied at more than a certain distance from itself. For example, referring to fig 8, the polypite might actively respond to irritation

Fig. 8.



of any point in the division d, e, f, g , while to irritation of any point in the division f, g, h, i its responses would be weaker, and to irritation of any point in h, i, j, k they would be very uncertain or altogether absent. Hence in this form of section we have reached about the limit of tolerance of which the non-radial connexions between the bell and polypite are capable*.

(e) Another interesting fact brought out by this form of section is, that the tracts occupied by the four radial tubes are tracts of comparatively high irritability as regards the polypite; for the certainty and vigour with which the polypite responds to a stimulus applied at one of the severed radial tubes fg, hi , or jk , contrast strongly with the uncertainty and feebleness with which it often responds to stimuli applied between any of these tubes. Indeed it frequently happens that a specimen which will not respond at all to a stimulus applied *between* the radial tubes fg , and hi , will respond certainly and well to a stimulus applied much further from the polypite, but *in the course of* the radial tube gk .

(f) And this leads us to another point of interest. In such a form of section, when

* This may also be well shown by the spiral form of section. Suppose fig. 2, Plate 30 to represent in a diagrammatic form a specimen of *Tiaropsis indicans* seen in projection from above. A spiral cut ABC is carried round as far as the point C, so as very nearly, though not quite, to overlap the beginning of the cut A. The polypite P may now actively respond to stimuli applied anywhere in the area A, B, C, D (although the response would probably be more active the nearer the stimulation to D). But if the cut be now carried to D, so as just to overlap A, all response on the part of P will cease to stimuli applied anywhere over the area ABC.

any part of the mutilated nectocalyx is irritated, the polypite shows a very marked tendency to touch some point in the tissue-mass *a a d e* (fig. 8) by which it still remains in connexion with the bell, and through which, therefore, the stimulus must pass in order to reach the polypite. And it is observable that this tendency is particularly well marked if the section has been planned as represented in fig. 8—*i. e.* in such a way as to leave the tissue-tract *a a d e* pervaded by a nutrient tube *d e*, this tube being thus left intact. When this is done the polypite most usually points to the uninjured nutrient-tube *d e* every time any part of the tissue-band *a l* is irritated*.

(*g*) Let us now very briefly consider the inferences to which these results would seem to point. The fact that the localizing power of the polypite is completely destroyed as regards all parts of the bell lying beyond an incision in the latter conclusively proves, as already stated, that all parts of the bell are pervaded by radial lines of differentiated tissue, which have at least for one of their functions the conveying of impressions to the polypite†. The fact in question also proves that the particular effect which is produced on the polypite by stimulating any one of these lines cannot be so produced by stimulating any of the other lines. Or, to state the same thing in the words previously used, we have conclusive proof that, so far as their *function* is concerned, these radial lines of differentiated tissue are undistinguishable from what we elsewhere know as afferent nerves. But although these tracts of differentiated tissue thus far resemble afferent nerves in their function, we soon see that in one important particular they differ widely from such nerves; for we have seen that, after they have been divided, stimulation of their peripheral parts still continues to be transmitted to their central parts, as shown by the non-localizing movements of the polypite. Of course this transmission cannot take place through the divided tissue-tracts themselves; and hence the only hypothesis we can frame to account for the fact of its occurrence is that which would suppose these tissue-tracts, or afferent lines, to be capable of vicarious action. Such vicarious action would probably be effected by means of intercommunicating lines, the directions of which would probably be various. In this way we arrive at the hypothesis of the whole contractile sheet being pervaded by an intimate plexus of functionally differentiated tissue, the constituent elements of which are capable of vicarious action in a high degree (see severity of section in fig. 8). And this hypothesis, besides being recommended by the consideration of its being the only feasible one that is open, is confirmed by the fact that the stimuli which it supposes to escape from a severed phalanx of radial lines, and thus

* It may here be stated that the greater sensitiveness of the nutrient tubes is also made apparent by the responses of the nectocalyx; for to a nip or prick of the general contractile sheet the response by the nectocalyx usually consists, as before stated, in a local bending in of the part irritated; whereas in response to similar irritation of a radial tube, the response is usually a general bending in of the whole nectocalyx—*i. e.* a general spasm.

I may here observe that cutting through all the nutrient tubes at their insertion in the polypite has no effect in preventing the localizing action of the latter as regards other parts of the bell.

† We must not, however, conclude that these lines are radial *structurally*; the evidence only proves that they are so *functionally*.

to reach the polypite after being diffused through many or all of the other radial lines (such stimuli thus converging from many directions), are responded to when they reach the polypite, not by any decided localizing action on the part of the latter, but, as the hypothesis would lead us to expect, by the tentative and apparently random motions which are actually observed. Moreover, we must not neglect to notice that these tentative or random movements resemble in every way the localizing movements, save only in their want of precision. Again, this hypothesis is rendered yet more probable by the occurrence of those *gradations* in the localizing power of the polypite which we have seen to be so well marked under certain conditions. The occurrence of such gradations under the conditions I have named is what the plexus theory would lead us to expect, because the closer beneath a section that a stimulus is applied, the greater will be the lateral spread of the stimulus through the plexus before it reaches the polypite. Similarly, the further the circumferential distance from the nearest end of such a section that the stimulus is applied, the greater will be its lateral spread before reaching the polypite. Lastly, the present hypothesis would further lead us to anticipate the fact that when *Tiaropsis indicans* is prepared as represented in fig. 8, the polypite refers a stimulus applied anywhere in the mutilated nectocalyx to the band of tissue by which it is still left in connexion with that organ; for it is evident that, according to the hypothesis, the radial lines occupying such a band are the only ones whose irritation the polypite is able to perceive; and hence it is to be expected that it should tend to refer to these particular lines a source of irritation occurring anywhere in the mutilated bell*.

It is not quite so clear why, in the last-mentioned experiment, the polypite should tend to refer a seat of irritation to the unsevered nutrient tube, rather than to the tracts

* It may be objected that the fact of diffused excitability persisting after destruction of the localizing function does not prove that the same tissue-elements are concerned in the two cases. For instance, in fig. 1, Plate 30, before introducing the cut *a*, a stimulus applied at *b* would, as before stated, cause localizing motion of the polypite. Let us call the tissue-tracts by which this localizing motion is effected *xx*, and let us call all the other tracts belonging to the same system, but occurring in other parts of the bell, *x'x'*. Now the hypothesis above explained supposes that after the cut *a* has been introduced, the random motions of the polypite which ensue on stimulating *b* are due to an escape of the stimulus at *a* from *xx* to *x'x'*, *i. e.* all over the bell. But the objector may ask, Why not suppose that the stimulus is conveyed to the polypite by some other tissue-element altogether, *e. g.* by *zz*, and hence that the function of the radial elements *xx* is exclusively that of enabling the polypite to localize correctly? Against this objection, of course, nothing can be urged, except that it merely suggests a possibility, and this a very improbable one. If such additional tissue-tracts are present, they must resemble those treated of in the text in at least one distinctive feature, *viz.* in having the property of conveying impressions to a distance. And forasmuch as the only objection to the above hypothesis consists in its supposing the distinguishing property of nerve to be blended with the property of vicarious action in a high degree, I cannot perceive any advantage in again supposing these properties blended in another tissue-element. On the contrary, any such additional supposition appears to me quite unnecessary, and, if accepted, would certainly serve but to render the explanation offered in the text more complicated than it is. Moreover the fact already alluded to in the text—*viz.* that tentative movements differ in no respect from the accurately localizing movements, except in their want of precision—this fact, I think, strongly tends to show that the same kind of tissue-elements is concerned in the production of all these movements.

of unsevered tissue on either side of that tube. The fact of its doing so, however, certainly seems to be connected with the fact of the radial tubes being tracts of high excitability. Now the latter fact, it seems to me, can only be accounted for in one of two ways. Either (*a*) we must suppose the course of a radial tube to coincide with that of a chain of ganglionic elements, or else (*b*) we must suppose it to coincide with something resembling a nerve-trunk—the latter being composed of aggregations of the afferent lines which we have already supposed to constitute the rudimentary nerve-plexus. According to the first of these suppositions, the comparatively high excitability of the radial tubes, as well as the pointing of the polypite to the unsevered tube in a specimen prepared as represented in fig. 8, would both be explained by the further supposition that when such a ganglion chain is stimulated—either directly or by conduction of the stimulus from a distance—the ganglionic elements discharge their influence, and so add to the strength of the original stimulus. According to the second of the above suppositions (*viz. b*), the fact of the high excitability of the nutrient tubes would be explained by the consideration that a stimulus applied to the supposed nerve-trunk would *directly* affect a greater *number* of the plexus-elements than would a stimulus applied to any other part of the bell. The additional fact to be met, *viz.* the pointing of the polypite to a single unsevered tube, is not quite so easy to explain on the present supposition; for if the assumed nerve-trunk is identical in function with a true nerve-trunk, the afferent elements collected in it ought to communicate to the polypite the impression of having had their *distal* terminations irritated; and therefore the fact of a number of such elements being collected into a single trunk ought not to cause the polypite to refer a distant seat of irritation to that trunk rather than to any of the parts from which the plexus-elements may emanate. Concerning this difficulty, however, I may observe that we seem to have in it one of those cases in which it would be very unsafe to argue with any confidence from the highly integrated nervous systems with which we are best acquainted to the primitive nervous systems with which we are now concerned. And although it would occupy too much space to enter into a discussion of this subject, I may further observe that I think it is not at all improbable that the polypite of *Tiaropsis indicans* should, in the absence of more definite information, refer a distant seat of injury to that tract of collected afferent elements through which it actually receives the strongest stimulation.

The first of these two suppositions (*viz. a*) will be found to derive some little support when we come to consider a curious class of facts to be dealt with in the next section. The second of these suppositions (*viz. b*) is supported by the histological researches of Professor HÆCKEL on *Geryonia*, a genus which closely resembles *Tiaropsis indicans* in form. This observer describes nerve-filaments following everywhere the course of the radial tubes, and receiving a number of minute filaments from either side. Moreover, the supposition we are now considering is further analogically supported by SCHULTZE's researches as to structure, and my own as to function, of the radial nerve-tracts in *Sarsia*.

On the whole, then, with regard to *Tiaropsis indicans*, I conclude in favour of something resembling a plexus of functionally-differentiated tissue-lines pervading the whole inner surface of the nectocalyx. A number of these tissue-lines I conceive to pursue, in a functional sense, a radial course; and, therefore, when intact, to enable the polypite correctly to localize a seat of irritation. Others of these lines I conceive to pursue various courses, and in so doing to connect the radial lines with one another. All the lines of such a plexus I conceive to be capable, in a high degree, of vicarious action; and I am inclined to suppose that a large proportional number of such lines are aggregated in the courses of the four radial tubes. But in now taking leave of the interesting series of facts which have led to these inferences, I should like to observe that, while I know the former cannot be modified by future investigation, I feel the latter may thus be shown imperfect or untrue. It has not seemed to me, however, that this is a sufficient reason to avoid speculation at the stage which my inquiries have now reached. There can be no doubt that the facts concerning *Tiaropsis indicans* are of a highly suggestive character; and I think it will shortly be found desirable thus to have paved the way towards arriving at some sort of conception with regard to analogous, though far more astonishing, facts which are presently to be adduced concerning *Aurelia aurita*.

§ 3. *Character of the Nervo-muscular Tissue of Staurophora laciniata*.—(a) The few individuals of this species which I was this year able to procure I utilized in the study of those peculiar spasmodic movements to which allusion was made in my former paper. These movements, it will be remembered, never occur spontaneously, but only in response to stimulation of certain parts of the organism, under which condition they never fail to occur. It will further be remembered that these spasmodic movements consist of a sudden and most violent contraction of the entire muscle-sheet, the effect of which is to draw together all the gelatinous walls of the nectocalyx in a far more powerful manner than occurs during ordinary swimming. In consequence of this spasmodic action being so strong, the nectocalyx undergoes a change in form of a very marked and distinctive character. The corners of the four radial tubes, being occupied by comparatively resisting tissue, are not so much affected by the spasm as are other parts of the bell; and they therefore constitute a sort of framework upon which the rest of the bell contracts—the whole bell thus assuming the form of an almost perfect square, with each side presenting a slight concavity inwards. These spasmodic movements, however, are quite unmistakable, even when they occur in a very minute portion of detached tissue; for however large or small the portion may be, when in a spasm it folds upon itself with the characteristically strong and persistent contraction. I say “*persistent* contraction” because it will be remembered that a spasmodic contraction, “besides being of unusual strength, is also of unusual duration.” That is to say, while an ordinary systolic movement only lasts a short time, a spasm lasts from six to ten seconds or more, and this whether it occurs in a large or in a small piece of tissue. Again, it will also be remembered that the diastolic movements differ very much in the case of an ordinary locomotor contraction and in that of a spasm; for while in the former case the process of relaxation is rapid even to sudden-

ness, in the latter it is exceedingly prolonged and gradual, occupying some four or five seconds in its execution, and, from its slow but continuous nature, presenting a graceful appearance. Lastly, the difference between the two kinds of contraction is shown by the fact that, while a spasm is gradually passing off, the ordinary rhythmical contractions may often be seen to be superimposed on it—both kinds of contraction being thus present in the same tissue at the same time.

(b) I have thus given a somewhat fuller description of these movements than that contained in my former paper, because, as the whole of the present section is to be occupied with their consideration, it seems desirable to render a complete account of them at the outset. Now the point with which we shall be especially concerned on the present occasion is one which has already been alluded to incidentally, viz. that in the case of *Staurophora laciniata* it is only stimulation of *certain parts* of the organism which has the effect of throwing it into a spasm. These parts are the margin (including the tentacles) and the courses of the four radial tubes (including the polypite, which in this species is spread over the radial tubes). This limitation, however, is not invariable; for I have often seen individuals of this species respond with a spasm to irritation of the general contractile tissue. Nevertheless, such response to such stimulation in the case of this species is exceptional—the usual response to muscular irritation being an ordinary locomotor contraction, which forms a marked contrast to the tonic spasm that *invariably* ensues upon stimulation of the margin, and *almost* invariably upon the stimulation of a radial tube. Still it must here be carefully noted, that in at least three other species belonging to another genus, viz. *Tiaropsis diademata*, *T. polydiademata*, and *T. oligoplocama*, spasmodic movements in no way distinguishable from those of *Staurophora laciniata* invariably follow upon stimulation of *any part of the organism*, or even of a minute portion of the contractile tissue when excised. Hence the usual failure of *Staurophora laciniata* to respond spasmodically to irritation of its contractile tissues is probably due to their being somewhat less irritable than those of the other species named.

(c) For my investigation of these spasmodic movements I chose *Staurophora laciniata* because, from its large size, it admitted of my performing various modes of section which would be impracticable in the case of the other naked-eyed Medusæ. Moreover, as the principal point to be inquired into had reference to the fact that these movements were most readily elicited by stimulating the marginal or radial tubes, this species seemed particularly well suited to the purposes of my inquiry; for, as we have just seen, the degree of its irritability is such as to cause the animal to respond spasmodically to the slightest irritation of the marginal or radial tubes, while even to violent irritation of the contractile tissues the only response is a locomotor contraction. The first point I endeavoured to settle was whether the faculty of originating a tonic spasm in answer to a stimulus was absolutely restricted, in the case of *Staurophora laciniata*, to the marginal and radial tubes, or such faculty was likewise shared by a small band of the contractile tissue in the immediate neighbourhood of these tracts.

To settle this point I tried gently pinching the margin with a fine pair of forceps: in answer to every nip I obtained a general spasm. I then tried nipping the general contractile tissue a millimetre or less from its line of junction with the marginal tissue: I obtained a general spasm. I next applied similar irritation two millimetres from the margin, and obtained no contraction of any kind on the part of the bell as a whole; but in the immediate neighbourhood of the irritation (*i. e.* about a quarter of an inch on either side of it) I obtained a *local* spasm. On now similarly irritating another point of the general contractile tissue, about another millimetre inwards from the margin, a still slighter local spasm was the result; and on repeating the experiment another millimetre or two from the margin no response of any kind was given. The same experiments were then conducted on one of the radial tubes, and they yielded the same results, with the exception that a general spasm was not of so certain occurrence in answer to nipping such a tube as it was in answer to nipping the margin. From these experiments, then, we see that there is no sharp line of demarcation between the tracts of tissue that are able to originate a spasm and those that are not. Nevertheless, I think the probability is that in these experiments the general and local spasms which resulted on irritating a point of the contractile tissue very near to one of these tracts, were really due to a slight sympathetic action on the part of the marginal or radial tube tissues which were so near to the actual point of irritation; for it must be remembered that such a local spasm could not have been obtained by irritating any other part of the general muscle-sheet of *Staurophora laciniata*.

(*d*) The next question I undertook to answer was the amount of section which the excitable tissues of *Staurophora laciniata* would endure without losing their power of conducting the spasmodic contraction from one of their parts to another. This was a very interesting question to settle, because, it may be remembered, *Staurophora laciniata*, like all the other species of discophorous naked-eyed Medusæ, differs from *Aurelia* &c. in that the ordinary contractile waves are very easily blocked by section*. It therefore became very interesting to ascertain whether or not the spasmodic wave admitted of being blocked as easily. First, then, as regards the margin. In my former paper I stated that if this be all cut off in a continuous strip with the exception of one end left attached *in situ*, irritation of any part of the almost severed strip will cause a responsive spasm of the bell, so soon as the wave of stimulation has time to reach the latter. This year, therefore, I continued this form of section into the contractile tissues themselves, carrying the incision round and round the bell in the form of a spiral, as

* As stated in the Postscript of my former paper, "there appear to be important differences between the discophorous naked-eyed Medusæ and the true *Discophora* in this respect; for in all the species of the former which I have as yet observed, the area of paralysis in the nectocalyx corresponds much more precisely with the line of ganglionic tissue which has been removed from its margin, than it does in the case of the true *Discophora*." I may here explain that this is not, of course, intended to mean that in no case is the spread of a contractile wave observable in the tissues of such naked-eyed Medusæ; but merely that such spread is usually far less extensive than it is in the case of the covered-eyed Medusæ.

represented in the case of *Aurelia* by Plate 33 of my previous paper. In this way I converted the whole Medusa into a ribbon-shaped piece of tissue*; and on now stimulating the marginal tissue at one end of the ribbon, a portion of the latter would go into a spasm. The object of this experiment was to ascertain how far into the ribbon-shaped tissue the spasmodic wave would penetrate. As I had expected, different specimens manifested considerable differences in this respect; but in all cases the degree of penetration was astonishingly great. For it was the exception to find cases in which the spasmodic wave failed to penetrate from end to end of a spiral strip caused by a section that had been carried twice round the nectocalyx; and this is very astonishing when we remember that the ordinary contractile waves, whether originated by stimulation of the contractile tissues, or arising spontaneously from the point of attachment of the marginal strip, usually failed to penetrate further than a quarter of the way round. But still more astonishing is the fact that these spasmodic waves will continue to penetrate such a spiral strip even after the latter has been submitted to a system of interdigitating cuts of a very severe description. Here, again, of course, considerable individual differences as to tolerance of section occur; but the drawing in Plate 30 (fig. 3) will convey some idea of the surprising amount of tolerance that is sometimes shown. This figure explains itself, it having been drawn to measurement from a specimen in which the spasmodic waves, started by stimulation of any point in the severed margin *ab*, would penetrate the whole of the strip *cde*, while in the same specimen the ordinary contractile waves became blocked at *d*.

(e) Now we have here to deal with a class of facts which physiologists will recognize as of a perfectly novel character. Why it should be that the very tenuous tracts of tissue which I have named should have the property of responding even to a feeble stimulus by issuing an impulse of a kind which throws the contractile tissues into a spasm; why it should be that a spasm, when so originated, should manifest a power of penetration to which the normal contractions of the tissues in which it occurs bear so small a proportion; why it is that the contractile tissues should be so deficient in the power of originating a spasm, even in response to the strongest stimulation applied to themselves—these and other questions at once suggest themselves as questions of the highest interest: at present, however, I am wholly unable to answer them. To assume that it is the ganglionic element in the margin, and possibly also in the radial tubes, which responds to direct stimulation by discharging a peculiar impulse which has the remarkable effect in question—to assume this is not to explain the facts. For the sake of rendering the matter quite clear, let us employ a somewhat far-fetched but convenient metaphor. We may compare the general contractile tissues of this Medusa to a mass of gun-cotton, which responds to ignition (direct stimulation) by burning with a quiet

* It may be stated that while conducting this mode of section on *Staurophora laciniata*, the animal responds to each cut of the contractile tissues with a locomotor contraction (or it may not respond at all); but every time the section crosses one of the radial tubes, the whole bell in front of the section and the whole strip behind it immediately go into a spasm.

flame, but to detonation (marginal stimulation) with an explosion. In the tissue, as in the cotton, every fibre appears to be endowed with the capacity of liberating energy in either of two very different ways; and whenever one part of the mass is made, by the appropriate stimulus, to liberate its energy in one of these two ways, all other parts of the mass do the same—and this no matter how far through the mass the liberating process may have to extend. Now, employing this metaphor, what we have to explain is why this capacity of dual response should exist in contractile tissues, and why certain slender lines of differentiated tissue should have the capacity, when themselves directly stimulated, of determining the explosive response. And to me it seems that neither of these questions is answered by supposing that it is the ganglionic element which, when itself directly stimulated, acts as a detonator. That this may be the case I do not dispute; for it is certainly, to say the least, a curious coincidence that such a marked differentiation of function as the facts imply should everywhere accompany and be restricted to the ganglionic tracts*; but what I desire to insist upon is this—that even if the ganglionic element could be proved to be the detonating element, the facts before us would not thus be accounted for. Doubtless it would be an interesting thing to know that a ganglion-cell may be able to originate two very different kinds of impulse, according as it liberates its energy spontaneously or in answer to direct stimulation†; but this knowledge would merely serve to transfer the questions which now apply to the marginal and polypite tissues in general to the ganglionic tissue in particular. Again, the supposition of the ganglia acting as detonators when themselves directly stimulated, would in no wise tend to explain why it is that the *contractile* tissues are capable of two such very different kinds of *response*. By detonating ordinary cotton, we can never obtain an explosion; and, similarly, unless the general contractile tissues of these Medusæ were in some way prepared to respond in a different manner to the different kinds of marginal or ganglionic discharge, we should never observe a spasm.

(*f*) Another solution of the difficulty may possibly present itself as worthy of consideration. Bearing in mind the facts already adduced with regard to the high degree

* As the polypite of *Staurophora laciniata* is spread out over the radial tubes, it is not improbable that ganglionic elements may here occur.

† It may perhaps be thought that this is too strong a statement. Considering that, in the various species of *Tiaropsis*, spasmodic motions result when any part of the irritable tissues are stimulated, it may appear that a spasm differs from an ordinary contraction only in the degree of its intensity; and therefore that, in *Staurophora*, direct stimulation of the ganglia is followed by a spasm only because a greater amount of ordinary ganglionic influence is thus caused to be liberated than would be the case in a merely spontaneous discharge. I think, however, that if this were the explanation there ought not to be so immense a contrast as there is between the facility with which a spasm may be caused by stimulation of the margin and of the contractile tissue respectively. The slightest nip of the margin of *Staurophora laciniata*, for instance, is sufficient to cause a spasm, whereas even crushing the contractile tissues with a large pair of dissecting-forceps will probably fail to cause any thing other than an ordinary contraction. Nevertheless, pricking the margin with a fine needle usually has the effect of causing only a locomotor contraction.

of sensitiveness manifested by the radial tubes of *Sarsia*, *Tiaropsis indicans*, &c., it may be suggested that if we imagine a vast number of nerve-tracts coursing from all parts of the bell towards the ganglionic tracts, we may imagine that on irritating any of these nerve-tracts near their central or ganglionic ends (nerve-trunks) a greater effect might be thus produced on the contractile tissues than could be produced by irritating the latter directly. In view of this possibility I tried making a V-shaped incision from the margin inwards, the angle of the V being situated about halfway between the centre and the circumference of the bell. The two sides of the V, however, did not quite meet at this angle, the effect of the section being thus almost, though not quite, to sever a wedge-shaped piece of tissue from the rest of the nectocalyx. Now on irritating the marginal tissue composing the thick end of this wedge, the latter went into a spasm, and, communicating the spasmodic wave through the very narrow tract of tissue at its thin end, it threw the whole nectocalyx into a spasm. This, of course, was what I expected, and from the mode of section it followed that the whole of the influence which caused the nectocalyx to go into a spasm must have passed through the narrow piece of tissue by which the wedge-shaped portion had been left in connexion with the rest of the nectocalyx. Yet, on waiting till the spasm passed off and then crushing with the forceps this narrow connecting piece of tissue, no response at all was given by the nectocalyx. This experiment, therefore, clearly shows that the nerve-trunk hypothesis will not account for the facts; because, as the hypothesis would require us to suppose that the entire nerve-supply by which the spasm-causing influence was conveyed to the nectocalyx passed through the narrow connecting piece of tissue, crushing this tissue ought, according to the hypothesis, to have produced a spasm; for at whatever point in the course of a nerve a stimulus is applied, the effect on the contractile tissue supplied by that nerve is the same*.

(g) There is one other fact worth stating with regard to this wedge-shaped form of section. Immediately after making the cuts which nearly but not quite sever the wedge-shaped mass, it is often observable that the *shock* suffered by the narrow connecting piece of tissue prevents it from conducting the spasmodic influence to the nectocalyx, the wedge itself alone going into a spasm. After a variable time, however, perhaps as long as a quarter of an hour, the conducting-power of the connecting-tissue is restored. But to produce this effect of shock, the connecting piece of tissue must be exceedingly narrow.

(h) In conclusion, I may state that anæsthetics have the effect of blocking the spasmodic wave in any portion of tissue that is submitted to their influence. It is always observable, however, that this effect is not produced till after spontaneity has been fully suspended, and even muscular irritability destroyed as regards direct stimulation. Up to this stage, the certainty and vigour of the spasm consequent on marginal irri-

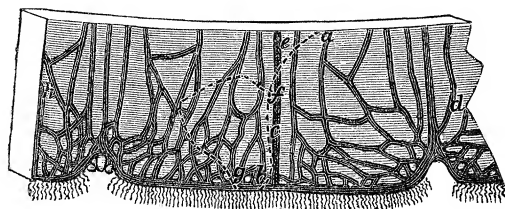
* The "avalanche" doctrine as to the summation of influence in a nerve appears to have become obsolete; but even if true it might be neglected in the above considerations—the supposed nerve-length being so small and the contrast between the effects of central and peripheral stimulation being so great.

tation are not perceptibly impaired; but soon after this stage the intensity of the spasm begins to become less, and later still it assumes a *local* character. It is important, also, to notice that at this stage the effect of marginal stimulation is very often that of producing a *general locomotor* contraction, and sometimes a series of two or three such. During recovery in normal sea-water all these phases recur in reverse order.

§ 4. *Character of the Contractile Tissues of Aurelia aurita.* (A) *Contractional Continuity.*—(a) This year I have been able to collect some additional facts relating to this subject; and of these facts the first that I shall deal with is an important one, namely, that exploration of the contractile tissues by graduated stimuli affords direct proof that these tissues are in a high degree functionally heterogenous. That is to say, if the swimming-bell of *Aurelia* be paralyzed by removal of its lithocysts, and if its irritable surface be then explored by induction-shocks of graduated intensity, differences in the excitability of different parts may thus be rendered clearly apparent. These differences are observable in all degrees, from being scarcely perceptible to being so pronounced that no strength of stimulation will cause any, except a very local, response. Moreover it is of importance for us to note that if the stimuli be administered by means of needle-point electrodes, it may almost always be observed that an area of low excitability does not graduate into an adjacent area of high excitability by successive stages, but that the one area is separated from the other by an exceedingly well-defined line of demarcation.

(b) Having observed these lines of demarcation between areas of different degrees of excitability to be so well defined, I was led to try cutting a spiral strip until the contractile waves became blocked, and then exploring the line of blockage by stimulus. In all cases I found that if I stimulated a fraction of a millim. on the spiral strip side of this line, the spiral strip responded, while the uncut portion of the bell remained passive; and, conversely, that if I stimulated the other side of this line, the uncut portion of the bell responded, while the spiral strip remained passive. To make the fact in question quite clear I may refer to fig. 9, which represents a portion

Fig. 9.



of a broad strip wherein the contractile waves became blocked at the curved line *a b*. On stimulating the tissue at any point as close as possible on one side of this line, as at *c*, a contractile wave would start from that point, and course all the way along the strip in the direction *c d*, but in that direction only; while if the stimulus were applied at any point on the other side of the line *a b*, as at *e*, the contractile wave thus originated

would course in the opposite direction $e h$, and in that direction only. On stimulating the line $a b$ itself, the result might either be no response at all, a contractile wave running in one direction, a contractile wave running in the other direction, or contractile waves running in both directions. These various results are doubtless to be explained by the various degrees in which the current escaped from the slender line $a b$.

(c) Exploration by stimulus, then, not only shows that different tissue-tracts differ in their degree of irritability; but also that they further differ in the degree of their permeability to the stimulating influence. In the cases just cited, viz. those of complete blocking, we perceive a total absence of this permeability; but it must now be stated that, just as in the cases previously cited of differential irritability, so in those of differential permeability there are all the degrees of difference observable. And, in the one set of cases as in the other, the lines of demarcation between adjacent areas are exceedingly well defined. For example, returning to our former sketch, the area enclosed by the line $b f$ and the angular line $b g$ was an area the minimal stimulation of any part of which was followed by a local contraction of the area $g b f$, while minimal stimulation of any point outside of the lines $g b f$ was followed by a general contraction of the entire strip situated outside of these lines. And of course there are other cases in which even the strongest stimulation of such an insular area as $g b f$ would fail to elicit any thing further than a local contraction of that area.

(d) From all this, then, we see that exploration by graduated stimuli reveals, first, differences in the degrees of excitability of closely contiguous tissue-areas, and, second, differences in the degrees of permeability to stimuli on the part of such areas—there being thus tissue-areas which admit of being more or less physiologically isolated from the rest of the tissue-mass by section. And the fact that in all these cases the lines of demarcation between the differentiated tissue-tracts are so sharply defined constitutes, I think, an additional support to the hypothesis concerning the presence of nerves, or “lines of discharge”*.

(B) *Excitational Continuity*.—(a) Closely related to this hypothesis are also the

* It has been suggested to me that contractile waves are merely muscle-waves, and that their blockage in contractile strips is due to shock. This, of course, would be a delightfully simple solution of the difficulties besetting this subject, and it is naturally the first one that occurs to an experimenter. But further observation shows that the tissues of Medusæ cannot be made to suffer shock unless the tissue-tracts affected by the section are exceedingly narrow, while blocking of contractile waves may take place in strips of considerable width. Moreover, the above results with regard to exploration by stimulus prove that even the *unmutilated* contractile tissues are far from being functionally homogenous. These results also negative the supposition which may possibly occur to some physiologists, viz. that blocking of the contractile waves in a spiral strip is due to a resistance that progressively varies with the length of the strip.

A more plausible explanation would be that the line of blocking is determined by an accidental strain to which that line has been previously subjected. That this is sometimes the case there can be no doubt, as the tissue bears optical indications of having been strained at the line of blocking. But that this cannot be the explanation in all cases is proved by the occurrence of those numerous gradations in different parts of the same tissue-mass, both with regard to excitability of tissue-areas and intimacy of physiological connexions.

facts to be detailed in this subsection. For if it can be proved that the contractile tissues of *Aurelia* are pervaded by tissue-tracts which display the essentially nervous function of establishing what I have termed excitational continuity between different parts, then I think we may be more prepared to believe that the passage of contractile waves depends on the presence of tissue-tracts presenting a nervous character. For the evidence being already in favour of the hypothesis that the passage of contractile waves depends on the presence of certain differentiated elements whose function is presumably nervous, such evidence would be further strengthened if it could be shown that in the very same tissue there occur other differentiated elements whose function is demonstrably nervous. Now that such elements as the last mentioned do occur in all parts of the excitable tissues of *Aurelia aurita* is a fact concerning which there can be no question.

(b) If any part of the polypite of *Aurelia* be stimulated, the natural rhythm becomes accelerated and the systoles more powerful. Again, if any part of the irritable surface of the swimming-bell be stimulated, not only do the swimming-motions become more rapid and powerful, but the lobes of the polypite writhe about in answer to the stimulation. These complementary facts clearly prove the occurrence of reflex action between the polypite and the swimming-bell reciprocally. Similarly, if seven lithocysts be removed, and the remaining one be of a somewhat weakly character, so as not to interfere with the observation by its excessive spontaneity, it may often be observed that if a portion of the irritable surface of the swimming-bell be submitted to a stimulus of somewhat less than minimal intensity as regards the starting of a contractile wave from the point of stimulation, a contractile wave will nevertheless start from the single remaining lithocyst so soon as time has been allowed for the stimulus to travel from the point of its application to that of the lithocyst. The greater the distance between these two points, the less certain is the experiment to succeed; but in many specimens it may succeed every time, even though the stimulus be applied at the opposite side of the swimming-bell from that in which the lithocyst is placed. In such cases, however, it is very important to observe that stimulation of certain tracts of tissue is followed by this reflex response, while stimulation of other tracts, even though these be situated much nearer to the lithocyst, is not so followed. Such excitable tracts are by no means constant as to their position in different individuals; but the fact of their occurrence tends to show that the reflex action we are contemplating is effected, not by means of an equally diffused excitability on the part of the whole nervo-muscular sheet, but by means of functionally differentiated tissue-tracts, which, during the experiment, act as afferent nerves.

(c) Next I must draw attention to a fact which will presently be proved of the highest importance in relation to the subject we are considering. It may be remembered, from Plate 32 in my former paper, that the entire margin of *Aurelia aurita* is fringed by a number of exceedingly delicate tentacles. These tentacles are highly retractile; and the point to which I have now to direct attention is this, that when any portion

of the irritable surface of *Aurelia* is stimulated *too gently to start a contractile wave*, it may nevertheless be sometimes observed that those tentacles which are nearest to the seat of stimulation respond with a sudden contraction, then those next adjacent to them on either side do the same, and so on—there being thus started in the margin two impulses which travel with equal rapidity in opposite directions, and the passage of which is marked by the successive and intensely sudden retraction of the numberless tentacles by which the margin is fringed. This most beautiful expression of the passage of a wave of stimulation does not occur in all, or even in most, specimens of *Aurelia*. It may best be seen in specimens that are perfectly fresh and vigorous—*i. e.*, in general, such as are deeply coloured. Moreover, just as in the case of reflex action, so in this case, the wave of stimulation may be started from some tracts more certainly than from others, although there is no constancy as to the position of these tracts in different individuals. As showing the identity of the wave of stimulation in this case and in that of reflex action, I may mention the following fact. When a single lithocyst is left *in situ* and a point in the nervo-muscular sheet at a distance from the lithocyst is gently irritated, if the passage of the stimulus happens to be marked by the above-described occurrence of what we may term a tentacular wave, it is always observable that the lithocyst never originates its reflex response until after the tentacular wave has reached it, and that it then invariably does so when the requisite period of latent stimulation has elapsed, viz. about half a second after the arrival of the tentacular wave. This experiment may be rendered particularly fascinating if the *Aurelia* has been previously cut into a broad strip, in such a way as to leave the single remaining lithocyst at one end; for on now irritating the other end of this strip, the tentacular wave may be observed to run continuously in the same direction all the way along the margin, and then, after it reaches the terminal ganglion and the period of ganglionic latency has elapsed, the contractile wave which it has been the means of starting from the ganglionic end of the strip courses all the way along the latter in the opposite direction to that which the tentacular wave had previously pursued.

In connexion with these tentacular waves I may further state that it does not signify how much of the tentacular rim is removed from the organism; for, however small a number of tentacles are left adhering to the margin, they exhibit the same action as when the whole series is intact.

(d) Now the occurrence of these tentacular waves is invaluable for the purpose of the experiments next to be described. These experiments consist in submitting the swimming-bell of *Aurelia* to various forms of section, with the view of ascertaining the extent to which the nervo-muscular tissues may be thus mutilated without suffering loss of their *excitational* continuity. The importance of any facts established by these experiments will doubtless be appreciated, in view of the theoretical standing of the analogous facts which we have so recently been considering with regard to *contractional* continuity. Of course the value of tentacular waves in these experiments consists in the circumstance that they never occur except in response to stimulation,

and that when they do occur they are of so unmistakable a character as to leave not the smallest room for supposing them due to any cause other than the passage of a stimulus.

The result of a number of experiments performed in this connexion is to show that the severity of section which causes blocking of the tentacular waves varies in different individual cases. Very frequently, however, the tolerance of tentacular waves towards section is quite as remarkable as is that of contractile waves. Or, adopting our previous terminology, section proves that in *Aurelia aurita* excitational continuity is as difficult to destroy as is contractional continuity.

To economize space, I shall not describe any of the intermediate degrees of tolerance, but shall pass at once to the most extreme instance which I have met with. The figure (see Plate 31) is one quarter life-size, and was carefully drawn to measurement*. It represents a specimen of *Aurelia aurita*, which, after having had its lithocysts removed, was cut in the same way as already described in the case of *Tiaropsis indicans* (fig. 8). The whole band-shaped length of tissue into which the swimming-bell was thus reduced was then submitted to the tremendously severe form of section which is represented in the figure. Yet on gently stimulating either end of the band-shaped tissue-mass *a b*, a tentacular wave would start from the point of stimulation, and, as represented in the figure, course all the way along the margin from end to end of the band-shaped mass†.

* *i. e.* the proportional length of the cuts was so drawn. When the animal is so severely mutilated, the swimming-bell floats out in various directions; so that in the Plate the general shape of the bell is to be regarded as diagrammatic.

† [In my MS., as it was originally sent to the Royal Society, there here followed some pages showing the confirmation which the above facts supplied to my view that the contractile tissues of *Aurelia* are pervaded by a nerve-plexus, the constituent fibres of which are capable of vicarious action in almost any degree. But as I have now, through Mr. SCHÄFER's collateral work, obtained microscopical demonstration of the presence of such a plexus, it becomes unnecessary to adduce the reasoning from function to structure which these pages contained, and I have therefore struck them out. It seems desirable, however, to quote from these omitted pages the following paragraph, which serves to state the present standing of the question as to whether the waves of contraction in *Aurelia* depend for their passage on the muscular elements alone, or likewise upon the nervous elements—a question which, it will be observed, is not decided even by the histological demonstration of a nerve-plexus:—

“But in addition to these general considerations we must remember, more particularly, that in *Aurelia aurita* we have already obtained evidence of more or less distinct conductile tracts—this evidence being even last year sufficiently strong to render the plexus theory on the whole the most probable one that could be devised. This year that evidence has been further confirmed by explorations by stimuli; so that the only obstacle in the way of our accepting the plexus theory to account for the passage of contractile waves is the enormous amount of section which the contractile tissues will endure without these waves becoming blocked. Now the only reason why this fact is an obstacle in the way of our accepting the plexus theory is because, upon that theory, this fact would require us to suppose the conductile elements to be capable of vicarious action to an almost incredible extent. Hence it was that last year the issue with respect to the passage of contractile waves lay between

§ 5. *Rate of Transmission of Stimuli in Aurelia aurita.* (A) *Contractile Waves.*—

(a) The rate at which contractile waves traverse spiral strips of *Aurelia* is variable. It is largely determined by the length and width of the strip, so that the best form of strip to use for the purpose of ascertaining the maximum rate is one which I shall call the circular strip. A circular strip is obtained by first cutting out the central bodies, *i. e.* polypite and ovaries, and then, with a single radial cut, converting the animal from the form of an open ring to that of a continuous band. I distinguish this by the name “circular” band or strip, because the two ends tend to preserve their original relative positions, so giving the strip more or less of a circular form. Such a strip has the advantage of presenting all the contractile tissue of the swimming-bell in one continuous band of the greatest possible width, and is therefore the form of strip that yields the maximum rate at which contractile waves are able to pass. The reason why the maximum rate should be the one sought for is because this is the rate which must most nearly approximate the natural rate of contractile waves in the unmutilated animal. This rate, at the temperature of the sea and with vigorous specimens, I find to be 18 inches per second.

(b) In a circular strip the rate of the waves is uniform over the whole extent of the strip; so that the time of their transit from one point to another varies directly as the length of the strip. But on now narrowing such a strip, although the rate is thus slowed, the relation between the narrowing and the slowing is not nearly so precise as to admit of our saying that the rate varies inversely as the width. The following figure will serve to show the proportional extent to which the passage of contractile waves is retarded by narrowing the area through which they pass:—

Fig. 10.

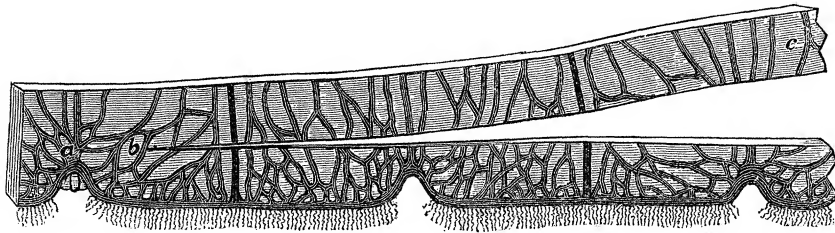
Time from end to end of a circular strip	
Time after width has been reduced to one half	
Time after width has been reduced to one quarter . .	
Time after width has been reduced to one eighth . . .	

regarding them as muscle-waves, notwithstanding the difficulties connected with their sudden blocking in spiral strips &c., or regarding their passage as due to nervous elements, notwithstanding the difficulties connected with the supposition as to vicarious action which this view necessarily involved. But this year it has been shown that these same tissues manifest a function essentially nervous, and that this function is as difficult to destroy by section as is that on which the passage of contractile waves depends. And forasmuch as this function cannot be regarded as muscular, we are in this case compelled either to adopt the hypothesis as to vicarious action of nerve-fibres, or to abandon the whole subject as inexplicable. Thus it is evident that these later results affect the previous ones to this extent, that they remove any advantage we should otherwise gain on the side of simplicity by regarding the contractile waves as mere muscle-waves; for, even if we do so regard them, we must still face the old difficulty in another form”—KLEINENBERG’S hypothesis as to the possible blending of the functions of nerve and muscle in the same tissue-elements having been shown, in a previous part of the omitted portion of this paper, to be here untenable.—September 1877.]

In such experiments it generally happens, as here represented, that reducing the width of a circular strip by one half produces no effect, or only a slight effect, on the rate, while further narrowing to the degree mentioned produces a conspicuous effect. I may also state that when, as occasionally happens, the immediate effect of narrowing a circular strip to one half is to temporarily block the contractile waves, when the latter again force their passage, their rate is slower than it was before. It seems as if the more pervious tissue-tracts having been destroyed by the section, the less pervious ones, though still able to convey the contractile wave, are not able to convey it so rapidly as were the more pervious tracts.

(c) In order to ascertain whether certain zones of the circular contractile sheet in all individuals habitually convey more of the contractile influence than do other zones, I tried a number of experiments in the following form of section. Having made a cir-

Fig. 11.

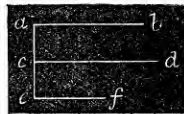


cular strip, I removed the lithocysts and then cut the strip as represented in fig. 11. On now stimulating the end *a*, the resulting contractile wave would bifurcate at *b*, and then pass on as two separate waves through the zones *b c*, *b d*. Now, as these two waves were started at the same instant of time, they ran, as it were, a race in the two zones and in this way the eye could judge with perfect ease which wave occupied the shortest time in reaching its destination. This experiment could be varied by again bisecting each of these two zones, thus making four zones in all, and four waves to run in each race. A number of experiments of this kind showed me that there is no constancy in the relative conductivity of the same zones in different individuals. In some instances the waves occupy less time in passing through the zone *b c* than in passing through the zone *b d*; in other instances the time in the two zones is equal; and, lastly, the converse of the first-mentioned case is of equally frequent occurrence. Very often the waves become blocked in *b c* while they continue to pass in *b d*, and *vice versa*. Now all these various cases are what we might expect to occur, in view of the variable points at which contractile waves become blocked in spiral strips &c.; for if the contractile tissues are not functionally homogenous, and if the relatively pervious conductile tracts are not constant as to their position in different individuals, the results I have just described are the only ones that could be yielded by the experiments in question. Considering, however, that in these experiments the central zones are not so long as the

peripheral zones, I think it may fairly be said that the conductile power of the latter is greater than that of the former; for otherwise the above experiments ought to yield a large majority of races won by the waves that course through the central zones; and this is not the case. Indeed it is surprising how often the race is, as it were, neck and neck, thus showing that the relative conductivity of all the zones is precisely adjusted to their relative lengths; and forasmuch as in the unmutilated animal this adjustment must clearly serve the purpose of securing to the contractile waves a passage of uniform rate over the whole radius of the umbrella, I doubt not that if it were possible to perform the racecourse section without interrupting any of the lines of conductile tissue, neck and neck races would be of invariable occurrence. It may be added that all the above results are observable when the discharges of a single remaining lithocyst are substituted for artificial stimuli at the undivided end of a strip.

(*d*) Interdigitating cuts, as might be expected, prolong the time of contractile waves in their passage through the tissue in which the cuts are interposed. For example, in a spiral strip measuring 26 inches in length, the time required for the passage of a contractile wave from one end to the other is represented by the line *ab* in the annexed woodcut. But after twenty interdigitating cuts had been interposed, ten on each side of the strip, the time increased to *cd*—the line *ef* representing one second. And more severe forms of section are, of course, attended with a still more retarding influence.

Fig. 12.

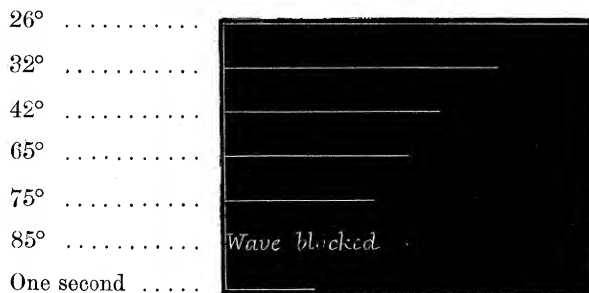


(*e*) The effects of temperature on the rate of contractile waves are very striking. For instance, in a rather narrow strip measuring 28 inches long and $1\frac{1}{2}$ inch wide, the following variations in rate occurred:—

Temperature of water.	Time occupied in passage of contractile waves.
26°	4 seconds.
32°	3 seconds.
42°	$2\frac{2}{5}$ seconds.
65°	2 seconds.
75°	$1\frac{3}{5}$ second.
85°	Blocked.

Or, adopting again the graphic method of statement, these variations may be represented as follows:—

Fig. 13.



(*f*) Submitting a contractile strip to slight strains has also the effect of retarding the rate of the waves while they pass through the portions of the strip which have been submitted to strain. The method of straining which I adopted was to pass my finger below the strip, and then, by raising my hand, to bring a portion of the strip slightly above the level of the water. The irritable, or contractile, surface was kept uppermost, and therefore suffered a gentle strain; for the weight of the tissue on either side of the finger made the upper surface somewhat convex. By passing the finger all the way along the strip in this way, the latter might be gently strained throughout its entire length, the degree of straining being determined by the height out of the water to which the tissue was raised. Of course if the strip is too greatly strained, the contractile waves become blocked altogether, as described in my last paper; but shortly before this degree of straining was reached, I could generally observe that the rate of the waves was diminished. To give one instance, a contractile strip measuring 22 inches had the rate of its waves taken before and after straining of the kind described. The result was as follows:—

Fig. 14.



Immediately after severe handling of this kind, the retardation of contractile waves is sometimes even more marked than here represented; but I think this may be partly due to shock; for on giving the tissue a little while to recover, the rate of the waves becomes slightly increased.

(*g*) Anæsthetics likewise have the effect of slowing the rate of contractile waves before blocking them. Taking, for instance, the case of chloroform, a narrow spiral strip 28 inches long was immersed in sea-water containing a large dose of the anæsthetic; the observations being taken at six seconds' intervals, the following were the results:—

Fig. 15.

Normal water	
Six seconds after transference to chloroform .	
Six seconds later	
Six seconds later	
Six seconds later	
Six seconds later	
One second	Wave blocked

In such experiments, the recovery of the normal rate in unpoisoned water is gradual. Taking, for instance, the case of a spiral strip in morphia:—

Fig. 16.

In normal water	
Quarter of an hour after exposure to morphia	
One minute after strengthening dose	
Four minutes later, and just before blocking of wave	
Fifteen seconds later, wave continuing blocked	Wave blocked
Immediately after passage of wave on restoration to normal sea-water	
Four minutes later	
Quarter of an hour later	
An hour later	
One second	

From this it will be seen that the original rate did not fully return. Some substances, however, exert a more marked permanent effect of this kind than do weak solutions of morphia. Here, for instance, is an experiment with alcohol:—

Fig. 17.

In normal water	
Quarter of an hour after exposure to weak dose	
Two minutes after strengthening of dose	
Five minutes later, and just before blocking of wave	
Fifteen seconds later, wave continuing blocked	Wave blocked
Immediately after passage of wave on restoration to normal sea-water	
An hour later	
One second	

(h) From these experiments, however, it must not be definitely concluded that it is the anæsthesiating property of such substances which exerts this slowing and blocking influence on contractile waves; for I find that almost any foreign substance, whether

or not an anæsthetic, will do the same. That nitrite of amyl, caffen, &c. should do so, one would not be very surprised to hear; but it would scarcely be expected that strychnine, for instance, should block contractile waves; yet it does so even in doses so small as only just to taste bitter. Nay, even fresh water completely blocks contractile waves after the strip has been exposed to its influence for about half an hour, and exerts a permanently slowing effect after the tissue is restored to sea-water. These facts show the extreme sensitiveness of the nervo-muscular tissues of the Medusæ to any change in the character of their surrounding medium—a sensitiveness which we shall again have occasion to comment upon when treating of the effects of poisons.

(i) In conclusion, I may mention an interesting fact which is probably connected with the summation of stimuli before explained. When a contractile strip is allowed to rest for a minute or more, and a wave is then made to traverse it, careful observation will show that the passage of this wave is slower than that of its successor, provided the latter follows the former after not too great an interval of time. The difference, however, is exceedingly slight, so that to render it apparent at all the longest possible strips must be used; and even then the experimenter may fail to detect the difference, unless he has been accustomed to signalling, by which method all these observations on rate have to be made.

(B) *Stimulus-waves*.—(a) The rate of transmission of tentacular waves is only one half that of contractile waves, viz. 9 inches a second. This fact appeared to me very remarkable, in view of the consideration that the tentacular wave is the optical expression of a stimulus-wave, and that there can be no conceivable use in a stimulus-wave being able to pass through contractile tissue independently of a contractile wave, unless the former is able to travel more rapidly than the latter; for the only conceivable use of the stimulus-wave is to establish physiological harmony between different parts of the organism; and if this wave cannot travel more rapidly than a contractile wave which starts from the same point, it would clearly fail to perform this function.

In view of this anomaly I was led to think that if the rate of the stimulus-wave is dependent in a large degree on the strength of the stimulus that starts it, the slow rate of 9 inches a second might be more than doubled, if, instead of using a stimulus so gentle as not to start a contractile wave, I used a stimulus sufficiently strong to do this. Accordingly I chose a specimen of *Aurelia* wherein the occurrence of tentacular waves was very conspicuous, and found, as I had hoped, that every time I stimulated too gently to start a contractile wave, the tentacular wave travelled only at the rate of 9 inches a second, whereas if I stimulated with greater intensity I could always observe the tentacular wave coursing an inch or two in front of the contractile wave.

(b) It is remarkable, however, that in this, as in all the other specimens of *Aurelia* which I experimented upon, the reflex response of the polypite was equally long whatever strength of stimulus I applied to the swimming-bell; or, at any rate, the time was only slightly less when a contractile wave had passed than when only a tentacular wave had

done so. The loss of time, however, appears to take place in the polypite itself, where the rate of response is astonishingly slow. Thus if one lobe be irritated, it is usually from four to eight seconds before the other lobes respond. But the time required for such sympathetic response may be even more variable than this, the limits I have observed being as great as from three to ten seconds. In all cases, however, the response, when it does occur, is sudden, as if the distant lobe had then for the first time received the stimulus. Moreover one lobe—usually one of those adjacent to the lobe directly irritated—responds before the other two, and then a variable time afterwards the latter also respond. This time is in most cases comparatively short, the usual limits being from a quarter of a second to two seconds. How much of these enormous intervals is occupied by the period of ganglionic latency, and how much by that of transmission, it is impossible to say; but I have determined that the rate of transmission from the end of a lobe of the polypite to a lithocyst (deducting a second for the double period of latent stimulation) is the same as the rate of a tentacular wave, viz. 9 inches a second. The presumption, therefore, is that the immense lapse of time required for reflex response on the part of the lobes is due to a prolonged period of latent stimulation on the part of the lobular ganglia, or whatever element it is that here performs the ganglionic function. And, in any case, it may be remarked, this wonderful tardiness of response on the part of the polypite of *Aurelia aurita* is strikingly similar to that of *Tiaropsis indicans*, where the rate of transmission of a stimulus in the bell, though very slow, is rapid as compared with the time that elapses before the polypite makes its sudden crouching movement. Both these cases, it will be noticed, stand in marked contrast with that of *Sarsia*, where response by the polypite to irritation of the bell or tentacles is exceedingly rapid.

V. COORDINATION.

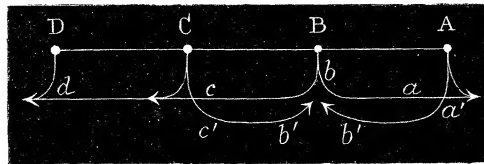
§ 1. *Covered-eyed Medusæ*.—(a) From the fact that in the covered-eyed Medusæ the passage of a stimulus-wave is not more rapid than that of a contractile wave, we may be prepared to expect that in these animals the action of the locomotor ganglia is not, in any proper sense of the term, a coordinated action; for if a stimulus-wave cannot outrun a contractile wave, one ganglion cannot know that another ganglion has discharged its influence, till the contractile wave which results from a discharge of the active ganglion has reached the passive one. And this I find to be usually the case; for, as previously stated, it may usually be observed that one or more of the lithocysts are either temporarily or permanently prepotent over the others, *i. e.* that contractile waves emanate from the prepotent lithocysts, and then spread rapidly over the swimming-bell, without there being any signs of coordinated, or simultaneous, action on the part of the other lithocysts. Nevertheless in many cases such prepotency cannot, even with the greatest care, be observed; but upon every pulsation all parts of the swimming-bell seem to contract at the same instant. And this apparently perfect coordination among the eight marginal ganglia may continue for any length of time. I believe, however, that

such apparently complete physiological harmony is not coordination properly so called, *i. e.* is not due to special nervous connexions between the ganglia; for, if such were the case, perfectly synchronous action of this kind ought to be the rule rather than the exception. I am therefore inclined to account for these cases of perfectly synchronous action by supposing that all, or most, of the ganglia require exactly the same time for their nutrition; that they are, further, of exactly equal potency in relation to the resistance (or excitability) of the surrounding contractile tissues; and that, therefore, the balance of force being exactly equal in the case of all, or most, of the ganglia, their rhythm, though perfectly identical, is really independent. I confess, however, that I am by no means certain regarding the accuracy of this conclusion, as it is founded on negative rather than on positive considerations. That is to say, I arrive at this conclusion regarding the cases in which such apparent coordination is observable only because in other cases such apparent coordination is *not* observable, and also, I may add, because my experiments in section have *not* revealed any evidence of nervous connexions capable of conducting a stimulus-wave with greater rapidity than a contractile wave. I therefore consider this conclusion an uncertain one; and its uncertainty is perhaps still further increased by the result of the following experiments. If a covered-eyed Medusa be chosen in which perfectly synchronous action of the ganglia is observable, and if a deep radial incision be made between each pair of adjacent ganglia, the incisions being thus eight in number and carried either from the margin towards the centre or *vice versa*, it then becomes conspicuous enough that the eight partially divided segments no longer present synchronous action; for now one segment and now another takes the initiative in starting a contractile wave, which is then propagated to the other segments. And it is evident that this fact tends to negative the above explanation; for if the discharges of the ganglia are independently simultaneous before section, we might expect them to continue so after section. It must be remembered, however, that the form of section we are considering is a severe one, and that it must therefore not only give rise to general shock, but also greatly interfere with the passage of contractile waves, and, in general, disturb the delicate conditions on which, according to the suggested explanation, the previous harmony depended. Besides, we have before seen that for some reason or other segmentation of a Medusa profoundly modifies the rate of its rhythm. In view of these considerations, therefore, the results yielded by such experiments must not be regarded as having any conclusive bearing on the question before us. And as these or similar objections apply to various other modes of section by which I have endeavoured to settle this question, I will not here occupy space in detailing them. It seems desirable, however, in this connexion again to mention a fact briefly stated in my former paper, namely, that section conclusively proves a contractile wave to have the power, when it reaches a lithocyst, of stimulating the latter into activity; for "it is not difficult to obtain a series of lithocysts connected in such a manner that the resistance offered to the passage of the waves by a certain width of the junction-tissue is such as just to allow the residuum of the contractile wave which emanates from one lithocyst to reach

the adjacent lithocyst, thus causing it to originate another wave which, in turn, is just able to pass to the next lithocyst in the series, and so on, each lithocyst in turn acting like a reinforcing battery to the passage of the contractile wave"*. Now this fact, I think, sufficiently explains the mechanism of ganglionic action in those cases where one or more lithocysts are prepotent over the others; that is to say, the prepotent lithocyst first originates a contractile wave, which is then successively reinforced by all the other lithocysts during its passage round the swimming-bell. In this way the passage of a contractile wave is no doubt somewhat accelerated; for I found, in marginal strips, that the rate of transit from a terminal lithocyst to the other end of the strip was somewhat lowered by excising the seven intermediate lithocysts.

(b) I may here state, in passing, a point of some little interest in connexion with this reinforcing action of lithocysts. When I first observed this action, it appeared to me a mysterious thing why its result was always to propagate the contractile wave in only one direction—the direction, namely, in which the wave happened to be passing before it reached the lithocyst.

Fig. 18.



For instance, suppose we have a strip A D with a lithocyst at each of the equidistant points A B C D. Suppose now that the lithocyst B originates a stimulus: the resulting contractile wave passes, of course, with equal rapidity in the two opposite directions, B A, B C (arrows $b a$, $b c$). The contractile wave $b a$ therefore reaches the lithocyst A at the same time as the contractile wave $b c$ reaches the lithocyst C; and so both A and C discharge simultaneously. What, then, should we expect to be the result? I think we should expect the wave $b c$ to continue on its course to D, after having been strengthened at C, and a *reflex* wave $a' b'$ to start from A (owing to the discharge at A) which would reach B at the same time as a similar *reflex* wave $c' b'$ starting from C (owing to the discharge at C); so that by the time the original wave $b c d$ had reached D, the point B would be the seat of a collision between the two reflex waves $a' b'$ and $c' b'$. And, not to push the supposed case further, it is evident that if such reflex waves were to occur, the resulting confusion would very soon require to end in tetanus. As a matter of fact, these reflex waves do not occur; and the question is, why do they not? Why is it that a wave is only reinforced in the direction in which it happens to be travelling—so that if, for instance, it happens to start from A in the above series, it is successively propagated by B C in the direction A B C D, and in that direction only, whereas, if it happens to start from D, it is propagated by the same lithocysts in the opposite direction, D C B A, and in that direction only?—the wave in the one case terminating at the

* Croonian Lecture, 1876, Phil. Trans. p. 311.

lithocyst D, and in the other case at the lithocyst A. Now, although this absence of reflex waves appears at first sight mysterious, it admits of an exceedingly simple explanation. It will be remembered, from my experiments on stimulation, that the contractile tissues of the covered-eyed Medusæ cannot be made to respond to two successive stimuli of minimal, or but slightly more than minimal, intensity, unless such stimuli are separated from one another by a certain considerable interval of time. Now, when in the above illustration the contractile wave starts from A, by the time it reaches B the portion of tissue included between A and B has just been in contraction in response to the stimulus from A, while the portion of tissue included between B and C has not been in contraction. Consequently the stimulus resulting from a ganglionic discharge being presumably of minimal, or but slightly more than minimal, intensity, the tissue included between A and B will not respond to the discharge of B; while the tissue included between B and C, not having been just previously in contraction, will respond; and conversely, of course, if the contractile wave had been travelling in the opposite direction.

(c) Seeing that this explanation is the only one possible, and that it, moreover, follows as a deductive necessity from my experiments on stimulation, I think there is no need to detail any of the further experiments which I made with the view of confirming it. But the following experiment, devised to confirm this explanation, is of interest in itself, and on this account I shall state it. Having prepared a contractile strip with a single remaining lithocyst at one end, I noted the rhythm exhibited by this lithocyst, and then imitated that rhythm by means of single induced shocks thrown in with a key at the other end of the strip. The effect of these shocks was, of course, to cause the contractile waves to pass in the direction opposite to that in which they passed when originated by the lithocyst. Now I found, as I had expected, that so long as I continued exactly to imitate the rate of the ganglionic rhythm, so long did the waves always pass in the direction B A—A being the lithocyst, and B the other end of the strip. I also found that if I allowed the rate of the artificially caused rhythm to sink slightly below that of the natural rhythm, after every one to six waves (the number depending on the degree in which the rate of succession of my induction-shocks approximated to the rate of the natural rhythm) which passed from B to A, one would pass from A to B*.

Of course the only interpretation to be put on these facts is, that every time an artificially started wave reached the terminal ganglion it caused the latter to discharge; but that the occurrence of a discharge could not in this case be rendered apparent, because of the inadequacy of that discharge to start a reflex wave. But that such discharges always took place was manifest, both *à priori* because from analogy we may be sure that if there had happened to be any contractile tissue of appropriate width on the other side of the ganglion, the discharge of the latter would have been rendered apparent, and *à*

* When two such waves met, they neutralized each other at their line of collision—or perhaps, more correctly, the tissue on each side of that line, having just been in contraction, was not able again to convey a contractile wave passing in the opposite direction to the wave which it had conveyed immediately before.

posteriori because, after the arrival of every artificially started wave, the time required for the ganglion to originate another wave was precisely the same as if it had itself originated the previous wave.

(d) In view of these results it occurred to me, as an interesting experiment, to try the effect on the natural rhythm of exhausting a ganglion thus situated by throwing in a great number of shocks at the other end of the strip. I found that after 500 single shocks had been thrown in with a rapidity almost sufficient to tetanize the strip, immediately after the stimulation ceased, the natural rhythm of the ganglion, which had previously been 20 in the minute, fell to 14 for the first minute, 18 for the second, and the original rate of 20 for the third. In such experiments the diminution of rate is most conspicuous during the first 15 or 30 seconds of the first minute. Sometimes there are no contractions at all for the first 15 seconds after cessation of the stimulating process; and in such cases the natural rhythm, when it first begins, may be as slow as one half or even one quarter its normal rate. All these effects admit of being produced equally well, and with less trouble, by faradizing the strip, when it may be even better observed how prolonged may be the stimulation without causing any thing further than such slight exhaustion of the ganglion as the above results imply*.

§ 2. *Naked-eyed Medusæ*.—(a) It would be impossible to imagine movements, on the part of so simple an organism, more indicative of physiological harmony than are the movements of *Sarsia*. One may watch several hundreds of these animals while they are swimming about in the same bell-jar, and never perceive, as in the covered-eyed

* In this description I have everywhere adopted the current phraseology with regard to ganglionic action—a phraseology which embodies the theory of ganglia supplying interrupted stimulation. But although I have done this for the sake of clearness, of course it will be seen that the facts harmonize equally well with the theory of continuous stimulation which I am engaged in working out, but the publication of which is for the present postponed. (See, for an outline of the new theory, the abstract of this paper in the Proc. R. S. vol. xxv.) Indeed the fact last mentioned in the text would agree with the new better than with the old theory of ganglionic action; for my other experiments on the deganglionated tissues of *Aurelia* prove how difficult these tissues are to exhaust. Hence if the natural rhythm in the case of the above-mentioned experiments is due to the contractile, as distinguished from the ganglionic, element, we should expect the period of quiescence between cessation of the faradaic stimulus and the renewal of spontaneity to be short; because this interval, according to the new theory, is the expression of the time required for the contractile tissue to recover exhaustion sufficiently to enable the ganglionic stimulation—which had become less than minimal in relation to the diminished excitability of the contractile tissue—to become minimal. I may also state that, according to the new theory, the reason why a contractile wave is reinforced while passing a lithocyst is probably the same as that to which all reflex action is by that theory supposed to be due, viz. the molecular disturbance in an afferent nerve being of the nature of a vibration, and the continuous somewhat less than minimal stimulation supplied by the ganglion being also of the nature of a vibration, if the wave-rates in these two vibrations are supposed *synchronous*, when the afferent disturbance reaches the ganglion the amplitude of the ganglionic vibrations would be somewhat increased. Hence the stimulation, which was previously being continuously supplied by the ganglionic vibrations, and which before being augmented by the arrival of the afferent vibrations was somewhat less than minimal, would now become minimal or somewhat more than minimal. And, conversely, the facts of *inhibition* are explained by this theory of ganglionic action as due to an *interference* of vibrations the rates of which are *not* synchronous.

Medusæ, the slightest want of ganglionic coordination exhibited by any of the specimens. Moreover, that the ganglionic coordination is in this case wonderfully far advanced, is proved by the fact of members of this genus being able to steer themselves while following a light, as described in my last paper*.

In the discophorous species of naked-eyed Medusæ, however, perfectly coordinated action is by no means of such invariable occurrence as it is in *Sarsia*; for although in perfectly healthy and vigorous specimens systole and diastole occur at the same instant over the whole nectocalyx, this harmoniously acting mechanism is very liable to be thrown out of gear; so that when the animals are suffering in the least degree from any injurious conditions—often too slight and obscure to admit of discernment—the swimming movements are no longer synchronous over the whole nectocalyx; but now one part is in systole while another part is in diastole, and now several parts may be in diastole while other parts are in systole. And, as in these animals very slight causes seem sufficient thus to impair the ganglionic coordination, it generally happens that in a bell-jar containing a number of specimens belonging to different species, numerous examples of more or less irregular swimming movements are observable†.

(b) Taking, then, the case of *Sarsia* first, from my previous observations on the physiological harmony subsisting between the tentacles, I was led to expect that the coordination of the locomotor ganglia was probably effected by means of the same tissue-tracts through which the intertentacular harmony was effected, viz. those situated in the margin of the bell. Accordingly, I introduced four short radial cuts, one midway between each pair of adjacent marginal bodies. The coordination, however, was not

* Removing the polypite does not interfere with this steering action; but if any considerable portion of the margin is excised, the animal seems no longer able to find the beam of light, even though one or more of the marginal bodies are left *in situ*.

† I think it is worth while to describe a peculiar irregularity of a very definite kind which is occasionally observable in *Tiaropsis diademata*. I have only noticed it in the case of tolerably vigorous specimens. It consists in the simultaneous contraction of two opposite quadrants of the nectocalyx, while the other two quadrants remain passive. The effect of the systole is therefore to convert the whole nectocalyx into an almost linear form. Diastole then follows as usual; but in the next systole the two quadrants which had previously been passive now contract, while the two which had previously contracted now remain passive. The nectocalyx, therefore, again assumes a linear form, but this time in a direction at right angles to that in which it had previously done so. Diastole then again ensues, and the third systole resembles the first one, the fourth the second, and so on—the nectocalyx alternately assuming the linear form in each of the two opposite directions. These peculiar motions may continue for a long time without interruption. Their rhythm is always perfect, and in its rate precisely resembles that which the same animal exhibits when swimming normally. The comparison is easily made, because every now and then the abnormal motions become suddenly converted into the normal ones, and *vice versa*. The time during which a normal or an abnormal bout continues is variable. The manifestation of such abnormal swimming-bouts appears to be an idiosyncrasy confined to a very small percentage of individuals; for, while one may observe a thousand specimens for any length of time without perceiving the occurrence of these peculiar movements, if there happens to be an additional specimen presenting the idiosyncrasy in question, every time the observer goes to look at it he may feel that there is about an equal chance of his seeing the normal or the abnormal movements.

perceptibly impaired. I therefore continued the radial cuts, and found that when these reached one half or two thirds of the way up the sides of the inner bell (or contractile sheet), the coordination became visibly affected, and this for the first time. These experiments, however, did not satisfy me that the coordination was not chiefly, or exclusively, due to the marginal nerves; for the bell of *Sarsia* is so small, and contractile waves are in this genus so rapid, that the following hypothesis still remained open. When the whole margin of *Sarsia* is removed and the paralyzed bell stimulated, so far as the eye can judge the resulting contraction is simultaneous over the entire bell. Whether this rapid conduction of contractile influence from the seat of stimulation to all the other parts of the bell is due to muscle or to nerve, is here of no consequence; for, in view merely of the fact of such rapid conduction taking place, it follows that when the four short radial cuts are introduced, even if these cuts destroy all the nerves by which the ganglionic coordination is effected, such coordination would still *appear* to be effected in consequence of the rapid conduction of a mere contractile wave over the whole muscle-sheet from the ganglion which first happens to discharge. And, if this is the correct interpretation, we should expect the loss of coordination first to become apparent when the radial incisions reach about halfway up the bell; for, under this form of section, it is then only that a stimulus applied to the margin of a *deganglionated*, or *paralyzed*, bell can be seen to cause in the bell a rapid contractile wave as distinguished from an apparently simultaneous contraction of the entire muscle-sheet. Against this interpretation it may be urged, that even although the discharge of a ganglion thus isolated from its fellows would certainly give rise to the erroneous appearance of a coordinated discharge of all the ganglia, still, if coordination is destroyed by the short radial cuts, we should expect this destruction to become observable in consequence of the ganglia in the four quadrants of the bell discharging independently of one another as to time, and therefore as a total effect producing a flurried movement of the bell, instead of the single decided systole followed by a short but perfectly inactive period of diastole. This objection, however, though natural, is not, I think, valid; for we have seen in the last section that, in the case of *Aurelia*, a contractile wave has the effect, when it reaches a locomotor ganglion, of causing the latter to discharge [§1(a)]; and the same thing is therefore presumably true in the case of *Sarsia*. Consequently, when in the latter genus ganglionic coordination has been destroyed by the four short radial cuts, and when any of the separated ganglia originates a discharge, all the other ganglia will immediately afterwards do the same, because stimulated by the passage of the contractile wave. Now, as all the ganglia were previously accustomed to act in consort, the time required for their nutrition after every discharge must be nearly or quite equal in the case of each of the ganglia; so that when, after the physiological harmony has been destroyed, one of their number originates a discharge, and when, as a consequence, all the others immediately afterwards do the same, the degree of exhaustion will be nearly or quite equal in the case of all the ganglia; and therefore the time that will elapse

before any of their number is again able to originate a discharge will be the same as if their physiological harmony had never been destroyed*.

In view of these considerations I tried the following experiments. Instead of beginning the radial cuts from the margin, I began them from the apex of the cone; and I found that however many of such cuts I introduced, and however far down the cone I carried them, so long as I did not actually sever the margin so long did all the divisions of the bell continue to contract simultaneously†. This fact therefore proves at least this much, that whether or not in the previous experiments true ganglionic coordination was effected through the upper zones of the bell, the margin of the bell is alone sufficient to maintain such coordination.

The next experiment I tried was to make four short radial incisions in the margin as before described, and then to continue *one* of these incisions the whole way up the bell. By careful observation I could now perceive that all the marginal ganglia did not discharge simultaneously; for when those situated nearest to the long radial cut happened to take the initiative, the resulting contractile wave, having double the distance to travel which it would have had if the long radial cut had been absent (or, as in the experiment described at the beginning of this subsection (*b*), if this radial cut had only been of the same length as the other three radial cuts), could now be followed by the eye in its very rapid course round the bell. Now the fact that in this form of section I was able to detect the passage of a *wave*, proves that the three short radial sections had destroyed the coordinated action of the marginal ganglia.

From these experiments, then, I conclude that in this genus ganglionic coordination, in the strict sense of the term, is effected exclusively by means of the marginal nerves. And as these experiments on *Sarsia* are exceedingly difficult to conduct, owing to the very rapid passage of contractile waves, it is satisfactory to find that this conclusion is further supported by the analogy which the other species of a naked-eyed Medusa afford, and to the consideration of which we shall now proceed.

(*c*) The effects of four short radial incisions through the margin of any species of *Tiaropsis*, *Thaumantias*, *Staurophora*, &c. are usually very conspicuous. Each of the quadrants included between two adjacent incisions shows a strong tendency to assume an independent action of its own. This tendency is sometimes so pronounced as to amount almost to a total destruction of contractional continuity between two or more quadrants of the bell; but more usually the effect of the marginal sections is merely that of destroying excitational continuity, or at least physiological harmony. In vigorous

* As in the last section, I adhere in the text to the current theory of ganglionic action; but the above considerations apply equally well on the new theory. These considerations are the same as have already been employed in an abridged form with reference to *Aurelia*, at the beginning of the last section.

† This could be particularly well seen if, after the extreme apex of the cone had been removed, one of the four radial cuts was continued through the margin, and the latter was then spread out into a linear form by gently pressing the animal against the flat side of the glass vessel in which it was contained. The same experiment performed on *Aurelia* is, of course, attended with a totally different result, now one segment and now another originating a discharge which then spreads to all the others in the form of a contractile wave.

specimens this effect is sometimes only observable, or best observable, at the commencement of a swimming-bout; for in such specimens, after a greater or less number of uncoordinated contractions, the four quadrants begin to agree, as it were, upon their rhythm. This, of course, is what might be expected on the above hypothesis regarding contractile waves eliciting ganglionic discharges, and all the ganglia requiring about the same time for their nutrition; and the reason why the loss of coordination under this form of section is more marked in the discophorous species of naked-eyed Medusæ than in *Sarsia*, is doubtless merely because the passage of contractile waves is so much more slow and so much less energetic. Therefore in vigorous specimens, where these waves pass more readily, we obtain results under this form of section most conformable to those which we obtain in *Sarsia*, viz. a sort of fictitious coordination which begins to come on after a variable number of contractions have been given, and which, as just stated, is doubtless due to the fact of all the marginal ganglia requiring the same time for their recovery from the exhaustion consequent on the occurrence of each discharge.

(d) It is a remarkable thing that this form of section, although in actual amount so very slight, is attended with a much more pernicious influence on the vitality of the organism than is any amount of section of the general contractile tissues. Thus if a specimen of *Tiaropsis*, for example, be chosen which is swimming about with the utmost vigour, and if four equidistant radial cuts only just long enough to sever the marginal canal be made, the animal will soon begin to show symptoms of enfeeblement, and within an hour or two after the operation will probably have ceased its swimming motions altogether. The animal, however, is not actually dead; for if, while lying motionless at the bottom of the vessel, it be gently stimulated, it will respond with a spasm as usual, and perhaps immediately afterwards give a short and feeble bout of swimming. These surprisingly pernicious results are not so conspicuous in the case of *Sarsia*, although in this genus likewise they are sufficiently well marked to be unmistakable. I here append a Table to show the comparative effects of the operation in question on different species. The cases may be regarded as very usual ones, though it often happens that a longer time after the operation must elapse before the enfeebling effects become so pronounced.

Name of species.	Number of contractions during five minutes before operation.	Number during one minute after operation.	Number during five minutes after operation.	Ultimate effects.
<i>Tiaropsis diademata</i>	57	11	0	Permanent rest.
—— <i>indicans</i>	148	23	0	" "
—— <i>polydiademata</i>	102	18	0	" "
—— <i>oligoplocama</i>	131	39	0	" "
<i>Sarsia tubulosa</i>	144	56	14	" "

This decided effect of so slight a mutilation will not perhaps appear to other physiologists so noteworthy as it appears to me; for no one who has not witnessed the experiments can form an adequate idea of the amount of mutilation of any parts, other than

their margins, which the Medusæ will endure without suffering even from the effects of shock. Another point worth mentioning with regard to the operation we are considering is that not unfrequently the interruptions of the margin, which have been produced artificially, begin to extend themselves through the nectocalyx in a radial direction; so that in some cases this organ becomes spontaneously segmented into four quadrants, which remain connected only by the apical tissue of the bell. I do not think that this is due to the mere mechanical tearing of the tissues as a consequence of the swimming motions, for the latter seem too feeble to admit of their producing such an effect.

(e) In conclusion, I may state that I have been able temporarily to destroy the ganglionic coordination of *Sarsia* by submitting the animals to severe nervous shock. The method I employed to produce the nervous shock without causing mutilation was to take the animal out of the water for a few seconds while I laid it on a small anvil, which I then struck violently with a hammer. On immediately afterwards restoring the Medusa to sea-water, spontaneity was found to have ceased, while irritability remained. After a time spontaneity began to return, and its first stages were marked by a complete want of coordination; soon, however, coordination was again restored. But this experiment by no means invariably yielded the same result. Spontaneity, indeed, was invariably suspended for a time; but its first return was not invariably, or even generally, marked by an absence of coordination, even though I had previously struck the anvil a number of times in succession. I was therefore led to try another method of producing nervous shock; and this I found a more effectual method than the one just described. It consisted in violently shaking the *Sarsia* in a bottle half filled with sea-water. I was surprised to find how violent and prolonged such shaking might be without any part of the apparently friable organism, except perhaps the tentacles and polypite, being broken or torn. The subsequent effects of shock were remarkable. For some little time after their restoration to the bell-jar, the *Sarsiæ* had lost, not only their spontaneity, but also their irritability; for they would not respond even to the strongest stimulation. In the course of a few minutes, however, peripheral or muscular irritability returned, as shown by responses to nipping of the nervo-muscular sheet. The animals were now in the same condition as when anæsthesiated by caffein or other central nerve poison; but in a few minutes later central or reflex irritability also returned, as shown by single responses to single nippings of the tentacles. Last of all spontaneity began to return, and was in some few cases conspicuously marked by a want of coordination—all parts of the margin originating impulses at different times with the result of producing a continuous flurried, or shivering, movement of the nectocalyx. After a time, however, these movements became coordinated; but in most cases when a swimming-bout had ended and a pause intervened, the next swimming-bout was always inaugurated by a period of shivering before coordination became established. This effect might last for a long time; but eventually it, too, disappeared—the swimming-bouts then beginning with coordinated action in the usual way.

VI. POISONS.

The last subject of which I shall treat in the present communication is the effects of various muscle- and nerve-poisons on the locomotor system of Medusæ. In my former paper I dealt briefly with this subject; but, having this year bestowed a considerable amount of additional labour upon it, I shall now discuss it at somewhat greater length. The subject appears to me one of considerable importance, seeing that the effects of the muscle- and nerve-poisons have never, as yet, been systematically tried on the Medusæ—animals that present us with the earliest appearance both of muscle and of nerve. I make this remark in order to excuse myself for burdening this already over-lengthy paper with a number of additional facts, which will be of interest only to the physiologist.

§ 1. *Chloroform*.—My observations with regard to the distribution of nerves in *Sarsia* led me to investigate the order in which these connexions are destroyed, or temporarily impaired, by anæsthetics. The results, I think, are worth recording. In *Sarsia*, then, the following phases always mark the progress of anæsthesia by chloroform &c.:—1. Spontaneity ceases, as described in my former paper. 2. On now nipping a tentacle, pulling the polypite, or irritating the bell, a *single* locomotor contraction is given in answer to every stimulation. (In the unanæsthesiated animal a *series* of such contractions would be the result of such stimulation.) 3. After locomotor contractions can no longer be elicited by stimuli, nipping a tentacle or the margin of the bell has the effect of causing the polypite to contract. 4. After stimulation of any part of the nectocalyx (including tentacles) fails to produce response in any part of the organism, the polypite will continue its response to stimuli applied directly to itself.

§ 2. *Nitrite of Amyl*.—On *Sarsia* the effect of this agent is much the same as that of chloroform—the description just given in § 1 being quite as applicable to the effects of the nitrite as to those of chloroform. Before the loss of spontaneity supervenes, the rate of the rhythm is increased, while the strength of the pulsations is diminished.

Tiaropsis diademata, from the fact of its presenting a very regular rhythm and being but of small size, is a particularly suitable species upon which to conduct many experiments relating to the effects of poisons. On this species the nitrite in appropriate (*i. e.* in very small) doses first causes irregularity and enfeeblement of the contractions, together with quickening of the rhythm. After a short time, a gradual cessation of the swimming-motions becomes apparent—these motions dying out more gradually, for example, than they do under the influence of chloroform. Eventually each pulsation is marked only by a slight contraction of the muscular tissue in the immediate neighbourhood of the margin. If the dose has been stronger, however, well-marked spasmodic contractions come on and obliterate such gradual working of the poison. In all cases irritability of all parts of the animal persists for a long time after entire cessation of spontaneous movements—perhaps for three or four minutes in not over-poisoned animals; but eventually it too disappears. On being now transferred to normal seawater, the process of recovery is slower than it is after anæsthesiation by chloroform. It is interesting, moreover, to observe, that just as the power of coordination was

the first thing to be affected by the nitrite, so it is the last thing to return during recovery.

§ 3. *Caffein*.—The effects of caffein on *Sarsia* may be best studied by immersing the animals in a saturated sea-water solution of the substance. In such solutions the Medusæ float to the surface, in consequence of their lower specific gravity. I therefore used shallow vessels, in order that the margins of the nectocalyces might rest in the level of the water that was thoroughly saturated. The immediate effect of suddenly immersing *Sarsia* in such a solution is very greatly to increase the rate of the pulsations, and, at the same time, to diminish their potency. The appearance presented by the swimming-motions is therefore that of a fluttering nature; and such motions are not nearly so effectual for progression as are the normal pulsations in unpoisoned water. This stage, however, only lasts for a few seconds, after which the spontaneous motions begin gradually to fade away. Soon they altogether cease, though occasionally one among a number of *Sarsia* confined in the same saturated solution will continue, even for several minutes after the first immersion, to give one or two very feeble contractions at long intervals. Eventually, however, all spontaneity ceases on the part of all the specimens; and now the latter will continue for a very long time to be sensitive to stimulation. At first *several* feeble locomotor contractions will be given in response to each stimulus; and as on the one hand these contractions never originate spontaneously, while, on the other hand, *paralyzed Sarsia* never respond to a single stimulus with more than a single contraction, these multiple responses must, I think, be ascribed to a state of exalted reflex irritability. After a longer exposure to the poison, however, only a single response is given to each stimulus; and still later all irritability ceases. On now transferring the *Sarsia* to unpoisoned water, recovery is effected even though the previous exposure has been of immensely long duration, *e. g.* an hour.

An interesting point with regard to caffein-poisoning of *Sarsia* is, that as soon as spontaneity ceases the tentacles and polypite lose their tonus and become relaxed to their utmost extent. This is not the case with anæsthesiation by chloroform, even when pushed to the extent of suspending irritability. If, however, *Sarsia* which have been anæsthesiated to this extent in chloroform be suddenly transferred to a solution of caffein, the tentacles and polypite may soon be seen to relax, and eventually these organs lose their tonus as completely as if the anæsthesia had from the first been produced by the caffein. Moreover in this experiment the irritability, which had been destroyed by the chloroform, returns in the solution of caffein—provided the latter be not quite saturated—though spontaneity of course remains suspended throughout.

The effects of graduating the doses of caffein may be stated in connexion with another species, viz. *Tiaropsis diademata*. In a weak solution the effects are a quickening of the pulsations (*e. g.* from 64 to 120 per minute) together with a lessening of their force. On slightly increasing the dose, the pulsations become languid, and prolonged pauses supervene. If the dose is again somewhat strengthened, the pulsations become weaker and weaker, till they eventually cease altogether. The animal, however, is now in a

condition of exalted reflex irritability; for its response to a single stimulus consists not merely, as in the unpoisoned animal, of a single spasm, but also, immediately after this, of a series of convulsive movements somewhat resembling swimming-movements destitute of coordination. If the strength of the solution be now again increased, a stage of deeper anæsthesiation may be produced, in which the Medusa will only respond to each stimulation by a single spasm. In still stronger solutions the only response is a single feeble contraction; while in a nearly saturated solution the animal does not respond at all. But even from a saturated solution *Tiaropsis diademata* will recover when transferred to unpoisoned water.

§ 4. *Strychnia*.—In my former paper I confined my remarks with reference to strychnia to the effects of this poison on a species of covered-eyed Medusa. It seems desirable, therefore, to supplement these remarks with a few additional ones regarding the effects of this poison on the naked-eyed Medusæ. In the case of *Sarsia* the symptoms of strychnia-poisoning are not well marked, from the fact that in this species convulsions always take the form of locomotor contractions. The symptoms, however, are in some respects anomalous. They are as follows:—First of all the swimming-motions become considerably accelerated, periods of quiescence intervening between abnormally active bouts of swimming. By-and-by a state of continuous quiescence comes on, during which the animal is not responsive to tentacular irritation, but remains so to direct muscular irritation, giving one response to each direct stimulus. The tentacles and polypite are much relaxed. In a sea-water solution just strong enough to taste bitter, this phase may continue for hours; in fact till a certain opalescence of the contractile tissues—which it is a property of strychnia, as of most other reagents, to produce—has advanced so far as to place the tissues beyond recovery. If the exposure to such a solution has not been very prolonged, recovery of the animal in normal water is rapid. In a specimen exposed for $2\frac{1}{2}$ hours to such a solution, recovery began in half an hour after restoration to normal water, but was never complete. In all cases, if the poisoning is allowed to pass beyond the stage at which response to direct muscular irritation ceases, the animal is dead.

On *Tiaropsis indicans* this poison has the effect of causing a general spasm, which would be undistinguishable from that which in this species results from general stimulation of any kind, were it not that there is a marked difference in one particular. For in the case of strychnia-poisoning the spasm, while it lasts, is not of uniform intensity over all parts of the nectocalyx; but now one part and now another part or parts are in a state of stronger contraction than other parts, so that, as a general consequence, the outline of the nectocalyx is continually changing its form. Moreover, in addition to these comparatively slow movements, there is a continual twitching observable throughout all parts of the nectocalyx. Each individual twitch only extends over a small area of the contractile tissue; but in their sum their effect is to throw the entire organ into a sort of shivering convulsion, which is superimposed on the general spasm. After a time the latter somewhat relaxes, leaving the former still in operation, which, moreover, now

assume a paroxysmal nature—the convulsions consisting of strong shudders and frequent spasms with occasional intervals of repose.

In the case of *Tiaropsis diademata* the action of strychnia is very similar, with the exception that there is no *continuous* spasm, although *occasional* ones occur amid the twitching convulsions. After a time, however, all convulsions cease, and the animal remains quiescent. While in this condition its reflex excitability is abnormally increased, as shown by the fact that even a gentle touch will bring on, not merely a single responsive spasm, as in the unpoisoned animal, but a whole series of successive spasms, which are often followed by a paroxysm of twitching convulsions. The condition of exalted reflex irritability is thus exceedingly well marked. Recovery in normal water at this stage is rapid, the motions being at first characterized by a want of coordination, which, however, soon passes off.

§ 5. *Veratrium*.—In *Sarsia* the first effect of this poison is to increase the number and potency of the contractions; but its later effect is just the converse, there being then prolonged periods of quiescence, broken only by very short swimming-bouts consisting of feeble contractions. The feebleness of the contractions gradually becomes more and more remarkable, until at last it is with great difficulty that they can be perceived at all; indeed the progressive fading away of the contractions into absolute quiescence is so gradual that it is impossible to tell exactly when they cease. During the quiescent stage the animal is for the first time insensible both to tentacular and to direct stimulation of the contractile tissues. That the gradual dying out of the strength of the contractions is not altogether due to the progressive advance of central paralysis, would seem to be indicated by the fact that contractions in response to direct stimulation of the contractile tissues are no more powerful at any given stage of the poisoning than are either responses to tentacular stimulation or the spontaneous contractions. Still, as we shall immediately see, in the various species of *Tiaropsis*, irritability persists after cessation of the spontaneous contractions. In *Sarsia* the nervous connexions between the tentacles and polypite, and also between the tentacles themselves, are not impaired during the time that the bell is motionless; and even when the irritability of the bell has quite disappeared as regards any kind of stimulation, the polypite and tentacles will continue responsive to stimuli applied either directly to themselves, or to any part of the nervo-muscular sheet of the bell.

The convulsions due to the action of veratrium are well marked in the various species of the genus *Tiaropsis*. They consist of violent fluttering motions without any coordination; but there are no spasms, as in the case of strychnia-poisoning. After the convulsions have lasted for some time, a quiescent stage comes on, during which the animal remains responsive to stimulation, though not abnormally so. Recovery in unpoisoned water is rapid, the movements being at first marked by an absence of coordination.

§ 6. *Digitalin*.—The first effect of this poison on *Sarsia* is to quicken the swimming-motions, and then to enfeeble them progressively till they degenerate into mere spasmodic

twitches. The polypite and tentacles are now strongly retracted, while the nectocalyx is drawn together so as to assume an elongated form. The latter is now no longer responsive either to tentacular or to direct stimulation; but the tentacles and polypite both remain responsive to stimuli applied either directly to themselves or to the nervo-muscular tissue of the bell. Death always takes place in very strong systole; and as this is an exceedingly unusual thing in the case of *Sarsia*, there can be no doubt that, in this respect, the action of the digitalin is different on the Medusæ from what it is on the heart.

On the various species of *Tiaropsis* digitalin at first causes acceleration of the swimming-movements, with great irregularity and want of coordination. Next strong and persistent spasms supervene, which give the outline of the nectocalyx an irregular form; and every now and then this unnatural spasm gives place to convulsive swimming-motions. Evidently, however, the spasm becomes quite persistent and excessively strong. The polypite of *Tiaropsis indicans* crouches to its utmost, and the animal dies in strong systole.

§ 7. *Atropin*.—In the case of *Sarsia* atropin causes convulsive swimming-motions. The systoles next become feeble, and finally cease. The nectocalyx is now somewhat drawn together in persistent systole, with the polypite and tentacles strongly retracted. Muscular irritability remains after tentacular irritability has disappeared, but it is then decidedly enfeebled.

In the various species of *Tiaropsis* the convulsions are strongly pronounced. They begin as mere accelerations of the natural swimming-motions, but soon grow into well-marked convulsions, consisting of furious bouts of irregular systoles following one another with the utmost rapidity, and wholly without coordination. Occasionally these movements are interrupted by a violent spasm, on which strong shuddering contractions are superimposed.

§ 8. *Nicotin*.—On dropping *Sarsia* into a sea-water solution of nicotin of appropriate strength, the animal immediately goes into a violent and continuous spasm, on which a number of rapidly succeeding minute contractions are superimposed. The latter, however, rapidly die away, leaving the nectocalyx still in strong and continuous systole; tentacles and polypite are retracted to the utmost. Shortly after cessation of spontaneity, the bell is no longer responsive to tentacular stimulation, but remains for a considerable time responsive to direct stimulation of its own substance; eventually, however, all irritability disappears, while the tentacles and polypite relax. On transferring the animal to normal water, muscular irritability first returns, and then central, as shown by the earlier response of the bell to direct than to tentacular stimulation; but if the animal has been poisoned heavily enough to have had its muscular irritability suspended, it is a long time before central irritability returns. Soon after central irritability has returned, the animal begins to show feeble signs of spontaneity, the motions being exceedingly weak, with long intervals of repose; but the degree of such feebleness depends on the length of time during which the animal has previously been exposed

to the poison; thus in a specimen which had been removed from the poison immediately after the disappearance of reflex irritability had supervened, recovery began in ten minutes after re-immersion, and was complete in half an hour.

In *Tiaropsis* the symptoms of nicotin-poisoning are also well marked. When gradually administered, the first effect of the narcotic is a complete loss of coordination in the swimming-motions. A slight increase of the dose brings about a tonic spasm, which differs from the natural spasm of these animals—(a) in being stronger, so that the nectocalyx becomes ball-shaped rather than square, (b) in being much more persistent, and (c) in undergoing variations in its intensity from time to time, instead of being a contraction of uniform strength; thus the spasm temporarily affects some parts of the nectocalyx more powerfully than other parts, so that the organ may assume all sorts of shapes. Such distortions proceed even further under the influence of nicotin than under that of strychnine, &c. Sometimes, for instance, one quadrant will project in the form of a pointed promontory; at other times two adjacent or opposite quadrants will thus project, and occasionally all four will do so, the animal thus becoming star-shaped. Sometimes, again, one quadrant will be less contracted than the other three, while at other times more or less slight relaxations affect numerous parts of the bell, its margin being thus rendered sinuous, though more or less violently contracted in all its parts. This state of violent spasm lasts for several minutes, when it gradually passes off, the nectocalyx relaxing into the form of a deep bowl and remaining quite passive, except that every now and then one part or another of the margin is suddenly contracted in a semilunar form. By-and-by, however, even these occasional twitches cease, and the animal is now insensible to all kinds of stimulation. Recovery in normal water is gradual, and marked in its first stage by the occasional retractions of the margin last mentioned. At about this stage also, or sometimes slightly later, the animal first becomes responsive to stimulation; and it is interesting to note that the response is performed, not by giving a general spasm as would the unpoisoned animal, but by folding in the part irritated—an action which very much resembles, on the one hand, the spontaneous convulsive movements just described, and, on the other, the response which is given to stimulation by the unpoisoned bell when gently irritated after removal of its margin. After these stages there supervenes a prolonged period of quiescence, during which the animal remains normally responsive to stimulation. Spontaneity may not return for several hours, and, after it does return, the animal is in most cases permanently enfeebled. Indeed, on all the species of Medusæ, nicotin, both during its action and in its subsequent effects, is the most deadly of all the poisons I have tried.

§ 9. *Alcohol*.—The solution must be strong to cause complete intoxication. The first effect on *Sarsia* is to cause a great increase in the rapidity of the swimming-motions—so much so, indeed, that the bell has no time to expand properly between the occurrence of the successive systoles, which, in consequence, are rendered feeble. These motions gradually die out, leaving the animal quite motionless. The nectocalyx is now

responsive to stimuli applied at the tentacles, and sometimes two or three contractions will follow such a stimulus, as if the spontaneity of the animal were slightly aroused by the irritation. Soon, however, only one contraction is given in response to every tentacular irritation, and by-and-by this also ceases—the Medusa being thus no longer responsive to central stimulation. It remains, however, for a long time responsive to stimulation of the nervo-muscle sheet; indeed the strength of the alcohol solution must be very considerable before loss of muscular irritability supervenes. It may thus be made to do so, however; and on then transferring the animal to normal water, recovery begins in from three minutes to a quarter of an hour. The first contractions are very feeble, with long intervals of repose; but gradually the animal returns to its normal state.

The above remarks apply also to *Tiaropsis*. In *T. indicans* the polypite recovers in normal water sooner than does the nectocalyx. Both in *Sarsia* and *Tiaropsis* the polypite and tentacles are retracted while exposed to alcohol, and, after transference to normal sea-water, the animals float on the surface—presumably in consequence of their having imbibed some of the spirit. The period during which floatation lasts depends, (*a*) on the strength of the alcohol solution used, and (*b*) on the time of exposure to its influence. It may last for an hour or more; but in no case is recovery complete till some time after the floatation ceases.

§ 10. *Cyanide of Potassium*.—On *Sarsia* the first effect is to quicken the contractions and then to enfeeble them. The animal assumes an elongated form, as already described under atropin. Spontaneity ceases very rapidly even in weak solutions; and for an exceedingly short time after it has done so, the bell continues responsive both to tentacular and to direct stimulation. For a long time after the bell ceases to respond to any kind of stimulation, the nervous connexions between the tentacles and between the tentacles and polypite remain intact, as also do the nervous connexions of these organs with all parts of the bell. This interesting fact is rendered apparent, first, by stimulating a tentacle and observing that all the four tentacles and the polypite respond; and, second, by irritating any part of the nervo-muscular sheet of the bell and observing that while the latter does not respond, both the tentacles and the polypite retract. Recovery from this stage occupies several hours.

In the case of *Tiaropsis* the convulsions are, as usual, more pronounced, being marked by the occurrence of a gradually increasing spasm, which differs from a normal spasm in the respects already described under strychnia. In all the species both of *Sarsia* and *Tiaropsis*, the polypite and tentacles are retracted during exposure to this poison.

§ 11. *Remarks*.—The above are some among the poisons which I have tried; but to avoid undue length I will not proceed further with the list on the present occasion. Enough, I think, has been said to show how surprising is the resemblance between the actions of these various poisons on the Medusæ and on the higher animals. When the physiologist bears in mind that in *Sarsia* we have the means of testing the comparative influence of

any poison on the central, peripheral, and muscular systems respectively *, he will not fail to appreciate the value of the foregoing observations. In reading over the whole list he will meet with an anomaly here and there; but, on the whole, I do not think he cannot fail to be satisfied with the wonderfully close adherence which is shown by these elementary nervous tissues to the rules of toxicology that are followed by nervous tissues in general. In one respect, indeed, there is a conspicuous and uniform deviation from these rules; for we have seen that in the case of every poison mentioned more or less complete recovery takes place when the influence of the poison has been removed, even though this has acted to the extent of totally suspending irritability. In other words, there is no poison in the above list which has the property, when applied to the Medusæ, of destroying life till long after it has destroyed all signs of irritability. What the cause of this uniform peculiarity may be is, of course, conjectural; but I may suggest two considerations which seem to me in some measure to mitigate the anomaly. In the first place, we must remember that in the Medusæ there are no nervous centres of such vital importance to the organism that any temporary suspension of their functions is followed by immediate death. Therefore, in these animals, the various central nerve-poisons are at liberty, so to speak, to exert their full influence on all the excitable tissues without having the course of their action interrupted by premature death of the organism, which in higher animals necessarily follows the early attack of the poison on a vital nerve-centre. Again, in the second place, we must remember that the method of administering the above-mentioned poisons to the Medusæ was very different from that which we employ when administering them to other animals; for, in the case of the Medusæ, the nervo-muscular tissue is spread out in the form of an exceedingly tenuous sheet, so that when the animal is soaking in the poisoned water every portion of the excitable tissue is equally exposed to its influence; and that the action of a poison is greatly modified by such a difference in the mode of its administration has recently been proved by Professor GAMGEE, who found that when a frog's muscle is allowed to soak in a solution of vanadium &c. it loses its irritability, while this is not the case if the poison is administered by means of the circulation.

In conclusion, I may observe that in the case of all the poisons I have tried, the time required for recovery after the animal is restored to normal water varies immensely. The variations are chiefly determined by the length of time during which the animal has been exposed to the influence of the poison, but also, in a lesser degree, by the strength of the solution employed. To take, for instance, the case of caffeine or chloroform, if *Sarsinæ* are transferred to normal water after they first cease to move, a few seconds are enough to restore their spontaneity; whereas if they are allowed to remain

* The method of comparison consists, as will already have been gathered from the perusal of the foregoing sections, in:—first, stimulating the tentacles, and observing whether this is followed by such a discharge of the attached ganglion as causes the bell to contract; next, stimulating the bell itself, to ascertain whether the muscular irritability is impaired; and, lastly, stimulating either the tentacles or the bell, to observe whether the reciprocal connexions between tentacles, bell, and polypite are uninjured.

in the poisoned water for an hour, they may not move for one or two hours after their restoration to unpoisoned water. In consequence of such great variations occurring from these causes, I was not able to compare the action of one poison with that of another in respect of the time required for effects of poisoning to pass away.

§ 12. *Fresh Water*.—As fresh water exerts a very deadly influence on the Medusæ, this seems the most appropriate place for describing its action. Such a description has already been given by Professor L. AGASSIZ, but it is erroneous. He writes:—"Taking up in a spoonful of sea-water a fresh *Sarsia* in full activity, when swimming most energetically, and emptying it into a tumbler full of fresh water of the same temperature, the little animal will at once drop like a ball to the bottom of the glass and remain for ever motionless—killed instantaneously by the mere difference of the density of the two media"*. As regards the appearance presented by *Sarsia* when subjected to "this little experiment," the account just quoted is partly correct; but Professor AGASSIZ must have been over-hasty in concluding that, because the animals seemed to be thus "killed instantaneously," such was really the case. Nothing, indeed, could be more natural than his conclusion; for not only is the contrast between the active swimming-motions of the *Sarsia* in the sea-water and their sudden cessation of all motion in the fresh water very suggestive of instantaneous death, but, a short time after immersion in the latter, their contractile tissues, as Professor AGASSIZ observed, become opalescent and whitish. Nevertheless, if he had taken the precaution of again transferring the *Sarsia* to sea-water, he would have found that the previous exposure to fresh water had not had the effect which he ascribes to it. After a variable time his specimens would have resumed their swimming-motions; and although these might have had their vigour somewhat impaired, the animals would have continued to live for an indefinite time—in fact quite as long as other specimens which had never been removed from the sea-water. Even after five minutes' immersion in fresh water, *Sarsia* will revive feebly on being again restored to sea-water, although it may be two or three hours before they do so; they may then, however, live as long as other specimens. In many cases *Sarsia* will revive even after ten minutes' exposure; but the time required for recovery is then very long, and the subsequent pulsations are of an exceedingly feeble character. I never knew a specimen survive an exposure of fifteen minutes†. In not a few cases, after immersion in fresh water, the animal continues to pulsate feebly for some little time; and, in all cases, irritability of the contractile tissues persists for a little while after spontaneity has ceased. The opalescence above referred to principally affects the polypite, tentacles, and margin of the nectocalyx. While in fresh water the polypite and tentacles of *Sarsia* are strongly retracted.

* Mem. American Acad. Arts and Sciences, 1850, page 229.

† The covered-eyed Medusæ survive a longer immersion than the naked-eyed—*Aurelia aurita*, for instance, requiring from a quarter to half an hour's exposure before being placed beyond recovery. Moreover the cessation of spontaneity on the first immersion is not so sudden as it is in the case of the naked-eyed Medusæ—the pulsations continuing for about five minutes, during which time they become weaker and weaker in so gradual a manner that it is hard to tell exactly when they first cease.

Thinking it a curious circumstance that the mere absence of the few mineral substances that occur in sea-water should exert so profound and deadly an influence on the nervo-muscular tissues of the Medusæ, I was led to try some further experiments to ascertain whether it is, as AGASSIZ affirms, to the mere difference in density between the fresh and the sea-water, or to the absence of the particular mineral substances in question, that the deleterious influence of fresh water is to be ascribed. Although my experiments lead to no very instructive conclusion, they are, I think, worth stating.

I first tried dissolving chloride of sodium in fresh water till the latter was of the same density as sea-water. *Sarsia* dropped into such a solution continued to live for a great number of hours; but they were conspicuously enfeebled, keeping for the most part at the bottom of the vessel, and having the vigour of their swimming-motions greatly impaired. The tentacles and polypite were strongly retracted, as in the case of exposure to fresh water, and the tissues also became slightly opalescent. Thinking that perhaps a fairer test would be only to add as much chloride of sodium to the fresh water as occurs in sea-water, I did so; but the results were much the same. On now adding sulphate of magnesium, however, to the amount normally present in sea-water, the *Sarsia* became more active. I next tried the effects of chloride of sodium dissolved in fresh water to the point of saturation, or nearly so. The *Sarsia*, of course, floated to the surface, and they immediately began to show symptoms of torpidity. The latter became rapidly more and more pronounced, till spontaneity was quite suspended. The animals, however, were not dead, nor did they die for many hours—their irritability continuing unimpaired, although their spontaneity had so completely ceased. The tentacles and polypite were exceedingly relaxed, which is an interesting fact, as being the converse of that which occurs in water containing too small a proportion of salt. Lastly, to give the density hypothesis a still more complete trial, I dissolved various neutral salts and other substances, such as sugar &c., in fresh water till it was of the density of sea-water; but in all cases, on immersing *Sarsia* in such solutions, death was as rapid as that which followed their immersion in fresh water.

VII. GENERAL SUMMARY.

The “fundamental experiment” of paralyzing nectocalyces by removing their margin has this year been repeated a vast number of times on various species of naked-eyed Medusæ, and always with the same result. In the case of the covered-eyed Medusæ, I have confirmed such of my previous observations as required confirmation, from the fact of their having been at variance with those of Dr. EIMER. I have continued to find that the lithocysts are the exclusive seats of spontaneity, so far as the “primary movements” are concerned. I have failed to detect the slightest evidence of spontaneity on the part of the contractile zones. I am still unable to say that the “secondary contractions” appear to me either more “feeble,” “inefficient,” or “local” than the primary ones; neither can I modify my previous statements as to the time during which these

secondary movements persist; for instead of "generally ceasing after a few moments" or "hours," they usually last for several days—in fact until the tissues begin to decompose. I am able, however, to agree with Dr. EIMER's statement that, other things equal, the unmutilated tissues preserve their irritability longer than those from which lithocysts have been removed; and I am able to agree with his statement that the rate of the natural rhythm has a tendency to bear an inverse proportion to the size of the individual, though I find that size is not the only factor in determining such rate. But his further statements with regard to the duration of the natural pauses bearing a direct proportion to the number and strength of the previous contractions, require, I think, to be taken with reserve; for both in *Aurelia* and in *Sarsia*, although a *general* relation of this kind may be observed, I have not found it to be so precise as Dr. EIMER affirms. Similarly, although it is true that the smaller segments of a divided *Aurelia* show a *general* tendency to contract less frequently than the larger segments, I have not found evidence of the precise relation which Dr. EIMER describes. On the other hand, I have found evidence of two additional factors which in these segmentation experiments are as important in determining the rate of the rhythm as is the size of the segments. These factors are (*a*) the potency of the lithocysts and (*b*) the time that elapses after the segmentation has been performed; for at first the smaller segments, if they contain prepotent lithocysts, have a quicker rhythm than the larger segments, but afterwards the rhythm of the former progressively slows more rapidly than does that of the latter. Although, however, the endurance is thus less in the case of a prepotent lithocyst in a small segment than is the endurance of less potent lithocysts in a large segment, the endurance of the former towards deprivation of oxygen is greater than is that of the latter; for, under such circumstances, the prepotent lithocyst will continue to act rhythmically in water which is stale enough to cause the less potent lithocysts to act irregularly, or not to act at all.

Other forms of mutilation—such as cutting off the polypite or portion of the swimming-bell—causes, first acceleration of the rhythm, and then a progressive decline to a certain point below the original rate. The rate then remains stationary at this point, but may again be made temporarily to rise and permanently to fall by removing another portion of the swimming-bell. In these experiments the rhythm, besides becoming permanently slowed, is also often rendered permanently irregular. Again, paring down the contractile tissues from around a single lithocyst has the effect, when the tissue is greatly reduced, of giving rise to enormously long periods of inactivity. During such a period, however, stimulation may initiate a bout of rhythmical contractions, to be followed by another prolonged pause. These facts tend to show that the apparently automatic action of the lithocysts is really due to a constant stimulation supplied by other parts of the organism.

Temperature exerts a profound influence on the rate of the rhythm. This influence may be best observed within moderate limits of variation; for water below 20° suspends spontaneity and even irritability, while water above 70° permanently slows the rhythm

after having temporarily quickened it. But water between 50° and 60° permanently quickens the rhythm during the time that Medusæ, which have been removed from colder water, are exposed to its influence. In very cold water the loss of spontaneity is a gradual though rapid process, as is also its return in warmer water. After having been frozen solid, *Aurelia* will recover on being thawed out, but the original rate of rhythm was not observed fully to return.

Oxygen accelerates the rhythm, while carbonic acid retards it, and in strong doses destroys both spontaneity and irritability. Deficient aëration of the water containing the Medusæ causes irregularity of their rhythm, as well as the occurrence of pauses. The latter become more and more pronounced the longer the water is left without being changed, till at last spontaneity altogether ceases; but on now restoring the animals to fresh sea-water, their recovery is surprisingly sudden.

As regards stimulation, I have proved that a few drops of hot water allowed to run over the excitable tissues of Medusæ cause a responsive contraction. Single mechanical or chemical stimuli applied to paralyzed swimming-bells of covered-eyed Medusæ frequently produces in response a small series of rhythmical contractions.

Light acts as a powerful stimulus to some species of Medusæ. Vigorous *Sarsia* respond to a single flash by entering on a bout of swimming; but less vigorous specimens only give a single contraction. The stimulus has been proved to be light *per se*, and not the sudden transition from darkness to light. Moreover a constant flood of light seems to act towards *Sarsia* as a constant stimulus. After removal of their marginal bodies, *Sarsia* no longer respond to luminous stimulation, while, on the other hand, any contractile tissue left adhering to the excised marginal bodies will continue to do so. *Tiaropsis polydiademata* responds to luminous stimulation as it responds to all other kinds of stimulation, viz. by going into a spasm; but the time that elapses between the occurrence of the stimulus and the occurrence of the response is very much longer in the case of luminous than in that of any other kind of stimulation. I find that this time is not, properly speaking, a period of latent stimulation; for a single flash requires to be of the same duration as a continuous flood of light in order to procure a response. Hence the period represents the time during which a certain summation of stimulating influence is taking place in the ganglia.

The period of latent stimulation in the case of *Aurelia* is greatly modified by certain conditions. Of these, temperature exerts the greatest influence; but, as a novel fact of great interest, the most important influence from a physiological point of view is that of the summation of stimuli, which, however, I need not again describe. At the bottom of a staircase the latent period is $\frac{5}{8}$ second, while at the top of a staircase it is only $\frac{3}{8}$ second. Summation of stimuli also greatly increases the amplitude of the contractions; so that it both develops in the tissue a state of expectancy and arouses it into a state of increased activity. My results in this connexion differ from those of Dr. BOWDITCH in that (*a*) the medusoid tissue has a shorter memory for the occurrence of a previous stimulation than has the cardiac; and (*b*) in the medusoid tissue a stimulus which at the bottom of a stair-

case is of less than minimal intensity, is able at the top of a staircase to give rise to a contraction of very nearly maximum intensity. This latter fact proves that the staircase action is, at any rate in part, dependent on the process of stimulation as distinguished from that of contraction. Moreover, that the effect is one pervading the whole extent of the irritable tissues, is proved by another fact, viz. that when at any stage during the construction of a staircase the electrodes are suddenly shifted to any other part of the irritable tissues, the next contraction will rank as the next step in the staircase. Other experiments have conclusively proved that the staircase action obtains in the case of the natural ganglionic stimulation in exactly the same way, both quantitatively and qualitatively, as it does in the case of artificial stimulation.

The excitable tissues of *Aurelia* may be thrown into tetanus by means of strong faradaic stimulation. That the tetanus is due to summation of contractions may be proved by throwing in single shocks at one end of a spiral strip with a key, and observing that if the shocks are thrown in with a certain rapidity, the resulting contractile waves overlap one another, so giving rise to persistent spasm. In such experiments, however long the strip may be, and however complicated the time relations between successive stimuli are made, whatever disturbances are set up at one end of the strip are faithfully transmitted to the other.

Reflex action has been proved to occur in various species of Medusæ. In *Sarsia* definite nervous connexions of constant occurrence have been shown to exist between the tentacles, but not between the tentacles and the polypite. Section of the nervo-muscular sheet proves that in the case of this genus physiological harmony may, as a rule, be easily destroyed, although it occasionally happens that such is not the case.

In *Tiaropsis indicans* the pointing action of the polypite is manifested by a portion of any size which may be cut from that organ. The ganglionic or localizing function is therefore diffused throughout the tenuous contractile tissues of the latter. This function admits of being destroyed, as regards any portion of the bell, by introducing a short incision between that portion and the base of the polypite; but after this the polypite, though no longer able to localize the seat of irritation, continues able to perceive that a stimulus is being applied in the bell somewhere. This shows that while the connexions on which the localizing function depend are radial, there are other connexions between the bell and polypite which are not radial. The latter connexions will endure a considerable amount of section before they are destroyed, particularly in the case of the tracts occupied by radial tubes. On carrying a spiral incision three fourths of the way round the nectocalyx, so as to leave one radial tube intact, and on then irritating any part of the spiral strip, it may be observed that the polypite usually points to the unsevered radial tube.

The spasmodic movements of *Staurophora laciniata* usually occur only when either the margin or the radial tubes are irritated. Although in this species ordinary contractile waves are easily blocked by section, spasmodic waves will continue to pass after very severe forms of section. Now it is a remarkable thing that the contractile tissues,

although themselves incapable of *originating* a spasm in response to stimulation, are nevertheless so wonderfully capable of *conducting* a spasm when this has been originated by irritation of the slender tissue-tracts above named. It is as though every fibre of the general contractile tissue were capable of liberating energy in either of two very different ways, and that whenever one part of the general mass is made to liberate its energy in one of these two ways, all the other parts of the mass do the same—and this no matter how far through the mass the liberating process may have to extend. And to say that it is the ganglionic element in the margin which, to recur to our previous metaphor, here acts as a detonator, is not to explain the facts; for although it would be an interesting thing to know that a ganglion-cell may be able to originate two different kinds of impulse according as it liberates its energy spontaneously or in answer to direct stimulation, this knowledge would merely serve to transfer the questions which now apply to the marginal and radial tube-tissues in general to the ganglionic tissues in particular. Again, the supposition of the ganglia acting as detonators when themselves directly irritated, would not explain why it is that the *contractile tissues* are capable of two such very different kinds of *response*. Anæsthetics block spasmodic waves, but not till they have suspended spontaneity, and even destroyed muscular irritability as regards direct stimulation.

In *Aurelia aurita* the passage of a tentacular wave marks the passage of a stimulus-wave. Such waves may be started more readily by stimulating some tracts than by stimulating others, though there is no constancy as to position of these tracts in different individuals. The case of stimulus-waves in this particular, therefore, resembles that of contractile waves, which, as explorations by graduated stimuli show, may also be more readily started from some tracts than from others. Again, the two cases resemble one another in the still more important particular of the astounding degree to which the tissues may be mutilated without their physiological connexions being destroyed. For excitational continuity being thus shown as difficult to destroy, in the case of this Medusa, as is contractional continuity, we are led to conclude, for reasons which I need not repeat, that both these functions are probably dependent on the same tissue-elements. And, in any case, the fact that the essentially nervous function of maintaining excitational continuity is able to persist in these primitive nervous tissues after they have been submitted to the severest possible forms of section, is a fact the significance of which, it seems to me, can scarcely be overrated. The fact itself cannot be explained by KLEINENBERG's theory of double-function cells; for sometimes contractile waves will become blocked by section before the tentacular waves, and sometimes *vice versa*. We seem, therefore, driven upon the theory of a nerve-plexus whose constituent elements are capable of vicarious action in almost any degree. This theory is supported by the results of explorations with graduated stimuli, and also by the consideration that in *Sarsia*, which is a more highly integrated form than *Aurelia*, the supposed plexus is so far differentiated that vicarious action on the part of its constituent elements is usually possible in but a low degree. Again, *Tiaropsis* appears to stand midway between *Sarsia* and

Aurelia in respect of the degree to which integration of its structures has advanced; and, as we have seen, it likewise occupies an intermediate position in respect of the degree in which vicarious action of the supposed nervous elements is possible.

Contractile waves in *Aurelia aurita* travel at the rate of 18 inches per second, if the temperature of the water is about that of the sea; but the rate is greatly modified by temperature, straining, anæsthetics, and various foreign substances. Stimulus-waves only travel at the rate of 9 inches per second, if the stimulus which starts such a wave is not strong enough at the same time to start a contractile wave; but if the stimulus is strong enough to start both waves, they both travel at about the same rate.

There appears to be no further coordination among the lithocysts of the covered-eyed Medusæ than such as arises from contractile waves coursing rapidly from one of the number and, as it passes the others, causing them successively to discharge; but, in the case of the naked-eyed Medusæ, true coordination has been proved to occur between the marginal ganglia, and the tracts through which it is effected have been proved to be the marginal nerves. Slightly cutting the margin of a naked-eyed Medusa exerts a very deleterious influence upon the vigour of the animal; and violent nervous shock, while it always suspends both spontaneity and irritability, will sometimes also destroy coordination for a considerable time after spontaneity returns.

The poisons whose effects I have described are chloroform, nitrite of amyl, caffeine, strychnia, veratrum, digitalin, atropin, nicotin, alcohol, and cyanide of potassium. The details of this part of the inquiry are rendered particularly interesting from the fact that in the case of *Sarsia* we have the means of testing the comparative influence of any poison on the central, peripheral, and muscular systems; but it is needless here to repeat details. In general, it will be remembered that the effects of the various poisons on these respective systems are almost uniformly such as occur in the case of the higher animals. In one important particular, indeed, the actions of nearly all the poisons differ from their actions on the higher animals; for there is no poison in the above list which has the property, when administered to the Medusæ, of destroying life till long after it has destroyed all signs of irritability. I have sought to explain this apparent anomaly by the considerations, first, that the Medusæ present to the action of the central-nerve poison no nerve-centres of vital importance to the organism; and, second, that my method of administering the poisons to the Medusæ was very different from that which is usually employed when administering these poisons to vertebrated animals.

Fresh water acts as a deadly poison to the Medusæ. The naked-eyed species usually cease their movements the instant they touch the fresh water, and are killed by it after an exposure of a few minutes; but the covered-eyed species are slightly more tolerant of its influence. The cause of this deadly influence exerted by fresh water depends on the absence of sea-water, and not on the difference of density between the former and the latter. Chloride of sodium alone, added in appropriate amount to fresh water, deprives the latter, to a very great extent, of its deleterious influence; but this is not the

case with any other substance which I have tried. Brine acts as an anæsthetic, and, in depriving the tentacles and polypite of their muscular tonus, exerts an effect the opposite of that which is exerted by fresh water.

POSTSCRIPT.

Having been in private correspondence with Prof. EIMER during the time that this paper was passing through the press, I now (April 9th, 1878) learn from him that all the differences which have hitherto existed between our statements admit of being reconciled. At his request, therefore, and in order to explain the character of the reconciliation, I append this Postscript.

The points wherein Prof. EIMER's observations did not perfectly agree with mine, or mine with his, were three in number:—

1st. We were not at one regarding the alleged rule that when an *Aurelia* is artificially segmented the rate of the rhythm which is manifested by each of the segments severally bears a direct proportion to the size of the segment, and this in a ratio such that the sum of the contractions which are performed by all the severed segments in a given interval of time is equal to the number of contractions which the unmutilated organism had previously performed in a similar interval of time. Dr. EIMER explains that further observation on his part has not tended to confirm this rule, and therefore that he desires his previous statements on this subject to be considered as withdrawn.

2nd. With regard to the character of the "secondary contractions" which always supervene in the covered-eyed Medusæ after removal of their lithocysts, our results have not hitherto been in full agreement. Dr. EIMER has described these contractions as irregular, inefficient, and feeble contractions, which are of a local nature and rarely last any considerable time after removal of the lithocysts—generally ceasing after a few moments, or, at any rate, after several hours. On none of these points did my observations altogether harmonize with this description, and I am therefore most glad to learn from Dr. EIMER that his further observations have now brought his views on all these points into precise agreement with my own.

3rd. Lastly, the difference of opinion which existed between us with regard to the exact seat of spontaneity in the covered-eyed Medusæ has also been happily removed. It appears that I have hitherto been under some misapprehension as to the precise area of tissue which Dr. EIMER intended to denote by his term "contractile zone;" for while I have hitherto supposed that by the term "contractile zone" Dr. EIMER intended to denote "the crescent-shaped interruption of the margin in which the lithocyst, together with its gelatinous hood, is situated"*, I now learn that I was incorrect in this supposition. From Prof. EIMER's letter I do not quite recognize the precise tissue-area which he endeavours to describe as the area to which his term "contractile zone" is

* Quoted from the Postscript to my Croonian Lecture, 1876, Phil. Trans. p. 309.

applicable; but this is a matter of no moment, as he leaves no doubt that the area in question is confined to what I may call the microscopical vicinity of the lithocyst. No doubt, therefore, the difference between our experimental results is to be attributed merely to the different manner in which we performed the operation of excising the lithocysts: for while conducting my experiments I supposed that the question which had to be settled was whether the spontaneity of the animal proceeded from the large "crescent-shaped interruptions" or from the very minute lithocysts; and, accordingly, in removing the latter alone, I was careful to remove them well *from* their roots—thus, no doubt, disturbing the "nerve-epithelium" which Mr. SCHÄFER has figured as occupying the microscopical vicinity of the lithocysts. On the other hand, Dr. EIMER, in conducting his experiments, must have had a completely different question in view, and therefore, in excising the lithocysts, he no doubt took scrupulous care to remove them well *above* their roots, so leaving the "nerve-epithelium" intact. Thus our apparent want of agreement on this point is shown to have arisen merely from a want of understanding with regard to the term "contractile zone."

It only remains for me to express my sincere satisfaction that the few and comparatively immaterial points with regard to which Prof. EIMER and myself were not previously quite agreed are thus so completely disposed of, and hence that in all respects our published results, in so far as they are common, are now in full accord.

G. J. R.

Fig. 1.

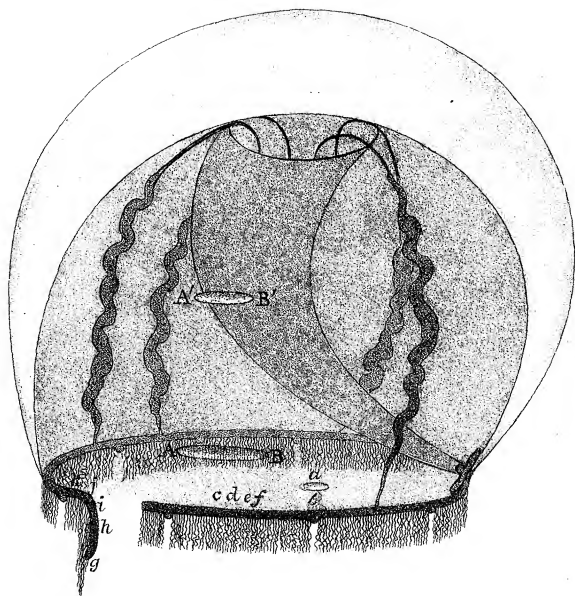


Fig. 2.

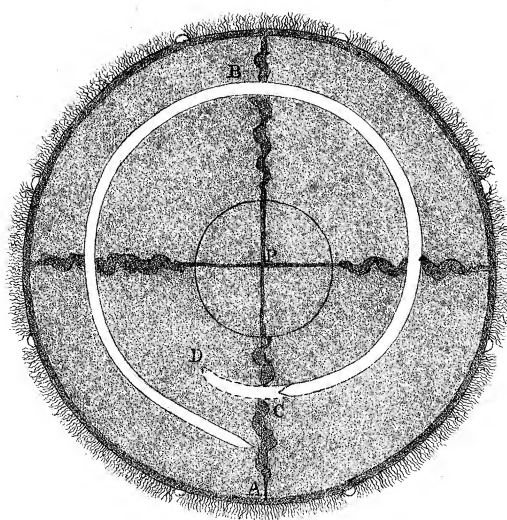


Fig. 3.

